

Establishing a baseline of plant diversity and endemism on a neotropical mountain summit for future comparative studies assessing upward migration: an approach from biogeography and nature conservation

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Abstract

Climate change is forcing many plant species to shift their range in search of adequate environmental conditions, being localized endemic species particularly at risk on mountain summits. The Pantepui biogeographic province, a set of flat-topped mountain summits (called *tepui*) of northern South America, contains both high plant diversity and high degree of endemism. Previous studies based on warming projections for the area suggested that half of the Pantepui endemic flora would disappear due to habitat loss by 2100. In this study, we selected one of the best-explored tepuis, Roraima-tepui, to establish the baseline of diversity and endemism for comparisons with historical data and future monitoring surveys, aimed at testing the hypothesis of upward migration of plants in response to global warming. We also analysed floristic and physiognomic features of the Eastern Tepui Chain (ETC, the mountain range where Roraima is located), and the phytogeographic patterns of both the ETC and Pantepui. The Roraima summit contains 227 species, including 44 new records, 13 exotic species (some of them with high invasive potential), and at least one species new to science. At the ETC level, Roraima is the tepui with highest species richness and degree of endemism, and shows a relatively high floristic similarity with Kukenán and Ilú. Herbaceous species dominate over shrubs on these tepuis, Tramen and Maringma, whereas on Yuruaní, Karaurín and Uei, they reach similar abundances. At the Pantepui level, endemic species have highly localized distribution patterns (17% local endemics). Conservation opportunities are evaluated in light of these results.

Keywords: Climate change; Floristic survey; Guayana region; Pantepui; Phytogeography; Plant invasion.

Introduction

Global warming is considered to be a major threat to high-mountain flora worldwide (Grabherr *et al.*, 2010). As a response to climate change, plants may shift their distribution (e.g., Pauli *et al.*, 2007; Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Feeley
55 *et al.*, 2011; Jump *et al.*, 2012), which can in turn produce the fragmentation or loss of their habitat (Thuiller *et al.*, 2005; Colwell *et al.*, 2008; Engler *et al.*, 2011). Those inhabiting summits could find themselves without suitable substrate; in the case of endemic species, extinctions would result in biodiversity loss on a global scale (Rull & Vegas-Vilarrúbia, 2006; Kreyling *et al.*, 2010; Dirnböck *et al.*, 2011). In addition, as
60 biotic responses are occurring at species level, changes in diversity and composition of many communities may also occur (Grabherr *et al.*, 2010; Walther, 2010; Sheldon *et al.*, 2011; Gottfried *et al.*, 2012; Pauli *et al.*, 2012). Tropical high-mountain biomes are of particular concern among biomes worldwide because of the high biodiversity and levels of endemism they harbour (Davis *et al.*, 1997; Myers *et al.*, 2000; Malcolm *et al.*,
65 2006; Rull, 2010; Laurence *et al.*, 2011; Nogué *et al.*, 2013). A way to empirically test predictions of global warming and the corresponding biotic responses is the periodic monitoring of selected plots, in order to verify whether their magnitude and rates square with the expected ones. In this regard, taxonomic research is essential for identifying, mapping, and predicting the biotic impacts of climate change. Standardized floristic
70 surveys are being increasingly used for that purpose in mountain environments, largely due to the existence of the GLORIA initiative (Global Observation Research Initiative in Alpine environments; <http://www.gloria.ac.at>), a long-term project with large-scale approaches, which has a goal of establishing and maintaining a worldwide network of observatories in order to document changes in high-altitude plant diversity related to
75 climate change (Grabherr *et al.*, 2000). In order to verify the existence of plant

migrations that may have already occurred in the last decades/century, some studies have used historic floristic surveys (Chou *et al.*, 2011; Stöckli *et al.*, 2011 and literature therein) or herbarium records (Feeley, 2011) to compare current species distribution with those of 40--100 years ago, providing positive results.

80 The neotropical Guayana Highlands constitute a singular high-mountain biogeographic province, located within the Guayana Shield region of northern South America. This discontinuous province, also called Pantepui, is formed by the assemblage of the summits (between 1500 and 3000 m elevation) of ~50 sandstone mountains, mostly table-like, locally referred to as *tepui* (Huber, 1995a). It stands out for its extraordinary
85 biotic differentiation with respect to the surrounding lowlands, especially of vascular plants (Huber, 1987). The difficulty to access the zone, together with the isolation of most tepui summits with respect to the lowlands have enabled the preservation for centuries from anthropogenic impacts of the unique flora of Pantepui. However, recent estimations based on the IPCC temperature projections for the area (Christensen *et al.*,
90 2007) suggest that, by the end of this century, an upward shift of environmental conditions of the order of 500 to 700 m would be expected (Rull & Vegas-Vilarrúbia, 2006), potentially resulting in the loss of >80% of the Pantepui's habitat (Vegas-Vilarrúbia *et al.*, 2012) and the extinction of the 30--50% of its endemic vascular flora (Nogué *et al.*, 2009; Safont *et al.*, 2012). As thoroughly discussed in previous studies
95 (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al.*, 2009; Rull *et al.*, 2009; Safont *et al.*, 2012), the consideration of temperature increases as the only environmental forcing and upward migration as the only biotic response is the main limitation of the analyses of habitat and biodiversity loss in Pantepui. Other factors like geological substrate and edaphic factors may have local importance (Huber, 1995a, 1995c), but the scarce
100 information available is a big handicap. Temperature is generally the main factor

controlling the altitudinal distribution of vascular plant species in Pantepui (Huber, 1995a) and in many other areas (e.g., Guisan & Theurillat, 2000; Thuiller *et al.*, 2005). In addition, precipitation is not expected to be as influential as temperature. Indeed, the 0--5% reduction in mean annual rainfall forecasted by the IPCC scenario by the end of this century (Christensen *et al.*, 2007) is almost negligible, considering the perhumid climate of the tepui summits.

In this study, Roraima-tepui, one of the currently best-explored tepuis with the oldest botanical collections of Pantepui, was selected for the following purposes: 1) to establish the baseline of diversity and endemism of vascular plants for future comparisons, aimed at testing the hypothesis of upward migration of plants in response to global warming; 2) to analyse floristic and physiognomic features of Roraima in the biogeographic context of the mountain range where it is located, the Eastern Tepui Chain (ETC) and Pantepui; 3) to verify the existence and state of exotic species transported by humans; and 4) to evaluate conservation opportunities, especially in light of the large number of ecotourists that visit the mountain summit annually.

Botanical inventories are key elements of monitoring programs aimed at testing the effects of climate change on the distribution and local abundance of plant species (Stöckli *et al.*, 2011). Our study is intended to be used for comparison with past floristic surveys or herbarium records of the Roraima summit, beginning in 1884, and as starting point for future monitoring of migratory phenomenon. Historical data do not provide as high a level of information as that provided by the GLORIA monitoring programs. However, to date it is the only method to document historical vegetation development in places where GLORIA-style monitoring has been absent (Feeley & Silman, 2011). Recently, the use of herbarium specimens combined with historic climatic data is gaining importance, as it also enables the examination of biotic

responses to climate change other than migration, such as those related to phenology (e.g., Calinger *et al.*, 2013). In addition to climatic changes, Roraima offers the possibility of testing the effect of direct anthropogenic impacts. As it is accessible by foot, it provides a ready means for the transportation and introduction of exotic species from surrounding lowland areas. Therefore, this study represents a baseline state against which changes in distribution and extension of species populations (either native or exotic) and vegetation formations can be assessed through time.

Subsequently, phytodiversity, endemism, and physiognomic patterns are compared among the tepui summits that shape the ETC. Dominant growth forms of most of the ETC summits were previously described by Huber (1995b). A contribution of this study is the determination of the abundances of the different physiognomic types at each summit of the ETC summits, which may provide important insights into their habitat diversity. Finally, phytogeographic patterns are analysed among the ETC and Pantepui. At the Pantepui level, previous studies used multivariate statistical methods to classify the tepuis according to their floristic composition, either considering the total set of Pantepui species (Riina, 2003) or only the endemics (Vegas-Vilarrúbia *et al.*, 2012). From these studies it was deduced that there were significant differences in the floristic composition among certain groups of tepuis, which were explained by the geographical distance among them, that is, their connectivity. Here, we use a revised and validated version of the raw data (Safont *et al.*, 2012) to obtain groups of species (clusters), whose relative abundances are determined for each tepui, and plotted on a map of the whole Pantepui area. Therefore, a graphical measure of floristic similarity is performed, that has implications for the interpretation of the degree of endemism within the Pantepui biome. At the ETC level, no previous studies exist addressing

phytogeographic patterns. Here, we calculate the floristic similarity and test the species-area relationship among its tepuis.

Study Area

Pantepui has been defined as a land archipelago (Rull, 2010), occupying an area of

approximately 6000 km². The majority of tepuis are located in southern Venezuela (Amazonas and Bolívar states), with some smaller ones in neighbouring areas of Brazil and Guyana (Fig. 1). They are the result of progressive erosion since

Jurassic/Cretaceous periods of the upper sedimentary rocks of the Guayana Shield

(Precambrian Roraima Group), leaving these remnants isolated from the surrounding

lowlands by spectacular cliffs (Briceño & Schubert, 1990) (Fig. 2). The nutritional poverty of the sandstone substrate and the limited drainage conditioned the development of nutrient-poor and anoxic soils. Under these conditions, decomposition of organic matter is incomplete, thus contributing to the accumulation of acids in the soil (Cuevas, 1992). Upper montane regions of Pantepui (1500--2400 m) have average annual air

temperature of 12--18 °C and average rainfall high to very high (2500--3500 mm). On the highest summits (>2500 m), climate is characterized by average annual air temperature around 10 °C or less (Huber, 1995a) and heavy rainfalls. Up to 5000 mm of annual rainfall have been estimated in the area of Roraima-Kukenán (Corrales, 2004).

Other characteristics of the highest tepui summits are dense cloud and mist formation

almost all year, frequent strong winds, and high solar radiation (Huber, 1995a).

Adiabatic decrease of average air temperature is 0.6 °C per 100 m altitude (Huber, 1995a). To date, more than 2400 plant species have been documented, of which 30% are endemic to Pantepui (Nogué *et al.*, 2009). According to the geographic discontinuities of Pantepui and physiognomic differences observed from aerial

reconnaissances, Berry *et al.* (1995) divided the province into four districts: East, West, Jaua-Duida, and South.

The ETC, one of the most important biogeographic units of Pantepui in terms of plant diversity and endemism, is located in the Eastern District, near and along the borders of southeastern Venezuela, central-western Guyana, and extreme northern Brazil (Fig. 3). It is comprised of 11 tepuis, 10 of which stretch in a roughly 70 km long arc from northwest to southeast, namely Tramen, Ilú, Karaurín, Wadakapiapué, Yuruaní, Kukenán, Roraima, Wei-Assipú, Yakontipú, and Maringma, and one disjunct tepui (Uei), situated 20 km to the southeast of the southern tip of Roraima (Table 1).

Tepui names were obtained from the *Flora of the Venezuelan Guayana* (FVG;

Steyermark *et al.*, 1995--2005) for the Venezuelan tepuis, and the topographic map of Guyana (The Survey Department of Guyana, 1975) for the Guyanan tepuis. According to these sources, summit elevations and areas range from 2000 m and 0.02 km² on Wadakapiapué to 2810 m and 34.4 km² on Roraima, the largest tepui of the group (Table 1). Roraima-tepui is situated at the triple boundary of Venezuela, Guyana and Brazil and is the tallest tepui of the Eastern District. Roraima's walls reach up to 700 m of vertical drop, and the slopes extend more than 1000 m until reaching the Gran Sabana and the lowland rainforests of Guyana and Brazil (Fig. 2). It is one of the icons of Canaima National Park, which covers almost 30,000 km² and was declared a World Heritage Site by UNESCO in 1994.

The oldest Pantepui botanical collections were made in 1838 on the southern slopes of Roraima by Robert H. Schomburgk, and four years later in the company of his brother, Richard M. Schomburgk. After that time several expeditions attempted to find a route to the summit, but it was not until 1884 that Everard F. Im Thurn and Harry I. Perkins succeeded. Then, during a scant few hours, they made the first collections of the

200 Roraima summit flora. The first significant collections, resulting from extended stays on
the summit, were made by Frederick V. McConnell and John J. Quelch (1894, 1898).
Subsequent expeditions that ascended to the ETC summits or high slopes by foot that
resulted in numerous botanical collections were those of Henry G.H. Tate (Roraima,
1927), Albert S. Pinkus (Roraima, 1929), Julian A. Steyermark (Roraima, 1944), and
205 Basset Maguire (Ilú, 1952; Uei, 1954-1955). A total of 31 expeditions were made to
Roraima through 1960, 12 of which were to the base and slopes and 19 to the summit.
From that year forward, expeditions with biological exploration purposes rose to 26 (3
to the slopes and 23 to the summit). Significant contributions were made by more recent
botanical expeditions via helicopter during 1976-1989 many of which were led by Otto
210 Huber (Ilú, 1984, 1985; Karaurín, 1987; Kukenán, 1984, 1985; Tramen-tepui, 1985;
Uei, 1985; Yuruaní, 1984, 1986). Additional explorations were conducted by Charles
Brewer Carías and the Terramar Foundation. Participating botanists on those trips were
Julian A. Steyermark (Roraima, 1976), Francisco Delascio C. (Ilú, 1977; Kukenán,
1977; Roraima, 1977, 1982, 1989; Tramen, 1989), and Ronald L. Liesner (Ilú,
215 Kukenán, and Roraima, 1988). Other plant collecting work by Venezuelan botanists
included Aníbal Castillo (Kukenán, 1982), Lionel Hernández (Yuruaní, 1983), Gabriel
Picón (Roraima, 1986), Hector Rodríguez (Roraima, 1988), and Fabián Michelangeli
(Roraima, 1992). H. David Clarke of the Smithsonian Institution and collaborators
climbed to the top of Maringma in 2004, providing the first records of plant species in
220 the ETC east of Roraima. The most recent botanical expeditions to the Roraima summit
were conducted as part of this study in 2011 and 2012, the results of which are included
in this study.

Methods

225 *Floristic inventory of the Roraima summit*

Field work consisted of exploring routes on foot across the summit, following existing trails but making every effort to traverse areas not previously explored by botanists. Given the rugged terrain atop Roraima, surveyed areas were limited by accessibility. Despite this, more than 80 linear km were covered, and our routes traversed the greatest
 230 possible variety of forest, shrubland, meadow, and epilithic vegetation formations. Expedition members spent a total of 24 days on the summit, during March 2011 and March 2012. Maximum and minimum elevations reached on the summit were 2770 and 2620 m, respectively.

Individual plants were identified *in situ* when possible (for approximately 50 of
 235 the well-known tepui species). Whenever there was uncertainty of identification, specimens were collected and photographed for subsequent study. A total of 374 collections were prepared, representing approximately 170 species. Collections were pressed in newspaper and preserved in 50% isopropyl alcohol. Subsequently, collected specimens were dried at 40--60 °C for 72 hours. We photographed living specimens of
 240 all the species found, as well as their habitats. In total, nearly 5300 photographs of plants were taken. Geographical coordinates of specimens and landmarks were recorded through a GPS device (Garmin eTrex Vista HCx and WGS84 datum), as well as with GPS-enabled digital cameras. Most taxonomic determinations were made by the authors and with the consultation of several taxonomic specialists (see acknowledgments). The
 245 first set of collections is deposited at VEN, with duplicates to be distributed to GUYN, SEL, BC, and those herbaria where specialists collaborating with the final identifications are based (at present, BRIT: Xyridaceae; CICY: Orchidaceae, F: Eriocaulaceae; MO: Asteraceae, Cyperaceae, Poaceae, Rubiaceae; NY: Ericaceae; UC: Pteridophyta).

We also conducted an extensive review of Venezuelan herbarium specimens, either directly (GUYN, MY, VEN), or through existing databases (CAR, MYF). Specimens deposited at foreign herbaria (F, K, MO, NY, UC and US) were consulted through a variety of online sources, especially through the Tropicos database (<http://www.tropicos.org>) and Smithsonian Institution's Biodiversity of the Guianas database. Finally, the inventory was completed through the revision of the comprehensive FVG, which was in turn used as the main taxonomic reference (except for few taxa that are recognized under a different classification system at the family level). For convenience, we recognize the families in three major working groups, Pteridophytes (including the Lycophytes), Dicotyledonae in the historical sense, and Monocotyledonae.

Assessment of exotic species

The floristic inventory was conducted in part to verify the existence and state of exotic species. For the purposes of this study, we applied the definition of exotic species provided by Richardson *et al.* (2000) and Pyšek *et al.* (2004) that classifies them as “those species whose presence in the study area is the result of either intentional or accidental human activity”. We also followed the nomenclature and definitions suggested by the same authors relating to the stages of the invasion process: casual exotic species, naturalized species, and invasive species. We considered the natural species range as the geographic area and elevations documented in the FVG (based on botanical collections from 1884 to 1995--2005, the period of preparation of the FVG). *In situ* observations of their habitat and degree of expansion were conducted, and a subsequent exhaustive bibliographic research was performed to determine their natural range and dispersal method.

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Floristic composition, physiognomy and phytogeographic patterns of the ETC summits

Floristic composition is defined as the degree of species diversity and endemism (Huber, 1995b). In our study, species diversity was expressed as species richness for each tepui summit, as well as for the ETC summits as a whole. Slopes were not
 280 considered as sufficient botanical information is unavailable at this time. As well, upper slopes (even above 1500 m) may contain species more likely representing the upland flora (Berry & Riina, 2005). The number of endemics was counted for each tepui, distinguishing several categories of endemism: local (single-tepui), ETC summits, ETC, Pantepui, and Guayana Shield. We also determined species of widespread distribution
 285 within the Neotropics, and exotic ones. Information on the species geographical and altitudinal ranges was derived from the distribution notes in the FVG, and when endemism was not clear from there, we checked the original specimens, mostly deposited at VEN, or revisions and monographs, which included the particular specimen collection information. As for physiognomy, growth forms were based on the FVG
 290 species descriptions (Huber, 1995b). Here, we excluded exotic species in order to compare native floras only. In addition, three tepuis were not included in this analysis as no floristic data are available for their summits, namely Wadakapiapué, Wei-Assipú, and Yakontipú.

To analyse the phytogeographic patterns, we calculated binary Sørensen
 295 similarity coefficients (SSC) (Jongman *et al.*, 1995) among tepuis, a commonly used measure to test the floristic similarity between sites, and the species-area relationship (MacArthur & Wilson, 1967) at the scale of the ETC summits. We did not include Karaurín due to insufficient floristic data. The power function was linearized through base-10 logarithm.

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Phytogeographic patterns in Pantepui

To analyse the phytogeographic relationships among tepuis at the Pantepui scale, we ran a Cluster analysis with Pantepui endemic species, as non-endemics may have phytogeographic relationships with other areas, obtaining a number of groups of related species (clusters). Subsequently, we calculated the relative abundances of each cluster in the floristic composition of each tepui, and represented them geographically on a Pantepui map to obtain a new measure of the floristic similarity among tepuis.

Raw data for this analysis were derived from a database based on the FVG, containing all available geographical and elevational information of the species occurring in the Pantepui biogeographic province (Pantepui database; Nogué *et al.*, 2009; Safont *et al.*, 2012). After discarding three endemic species due to the lack of detailed distribution information, a total of 626 endemic species were computed. We considered 43 tepuis that contained endemic species. However, some of them were treated as a single tepui due to its physical connection above 1500 m (the lowermost boundary of Pantepui) or for which had aggregated distributional data in the FVG. These tepuis are: Roraima, Kukenán, and Yuruaní; Karaurín, Ilú, and Tramen; Carrao and Ptarí; Kamarkawarai, Tereké-Yurén, Murisipán, and Aparamán (Los Testigos massif); Auyán, Cerro El Sol, and Cerro La Luna (Auyán massif); all tepuis of the Chimantá massif; Yutajé and Coro Coro; and Aracamuni and Avispa. Therefore, the effective number of tepuis used for the analysis was 31. These data were entered into PAST software, version 2.16 (Hammer *et al.*, 2001) to develop the Cluster analysis, in which species were classified according to unweighted pair-group average (UPGMA) algorithm and Raup-Crick similarity measure for presence-absence data, ranging from 0 to 1 (Raup & Crick, 1979). Unlike the Sørensen coefficient (previously used by Vegas-

Vilarrúbia *et al.*, 2012), this measure uses a randomization (Monte Carlo) procedure, comparing the observed number of species occurring in both associations with the distribution of co-occurrences from 1000 random replicates from the pool of samples. Clusters of species were defined as groups of species with Raup-Crick similarity measure above 0.7.

Results

Inventory of the vascular flora of the Roraima summit

The Roraima summit flora includes 51 families, 130 genera, and 227 vascular plant species. Of them, 201 (88.5%) were observed during our fieldwork. Among

Pteridophyta, 15 families, 31 genera and 70 species were recorded. In the traditional Angiospermae, Dicotyledonae are represented by 26 families, 54 genera and 81 species, and Monocotyledonae by 10 families, 45 genera and 76 species. No Gymnospermae representatives were found either in the field or in herbaria. At family level, Orchidaceae is the most diverse, with 15 genera and 26 species, followed by Grammitidaceae, Asteraceae, Cyperaceae, Bromeliaceae, Dryopteridaceae, Poaceae, Ericaceae, and Pteridaceae (Table 2). These nine families together contain nearly half of the species and genera reported for the summit. At the genus level, *Elaphoglossum*, *Epidendrum*, *Xyris*, *Octomeria*, *Peperomia*, *Pterozonium*, and *Utricularia* are the most species-rich, representing 18.1% of the total. A complete list of the vascular flora of the Roraima summit is shown in Online Resource 1.

Our collections and extensive herbarium surveys yielded 44 novelties for the Roraima summit flora since the publication of the FVG, representing a 24% increase with respect to the original compilation of that work (Steyermark *et al.*, 1995--2005). These include 15 species that we could not match with historically collected taxa from

350 Roraima and are in further need of study by specialists. They are indicated in Online
 Resource 1 as 'sp.' At least one of these has been identified as a species new for
 science, the orchid *Epidendrum* sp. (G. Carnevali, personal communication). Five
 families of plants were collected for the first time on the summit, Juncaceae,
 Rhamnaceae, Rosaceae, Solanaceae, and Symplocaceae, as well as 15 genera
 355 (Asteraceae: *Gnaphalium*, *Mikania*, *Sonchus*; Ericaceae: *Sphyrospermum*;
 Melastomataceae: *Tibouchina*; Bromeliaceae: *Lindmania*, *Racinaea*; Cyperaceae:
Eleocharis; Orchidaceae: *Elleanthus*, *Eriopsis*, *Gomphicis*; Poaceae: *Avenella*, *Cinna*,
Vulpia; and Dennstaedtiaceae: *Paesia*). Finally, 14 taxa collected represent new
 additions for the Roraima summit flora at the species level (Asteraceae: *Stenopadus*
 360 *sericeus*; Lentibulariaceae: *Genlisea repens*, *Utricularia pubescens*; Piperaceae:
Peperomia rotundata; Rubiaceae: *Psychotria aubletiana*; Cyperaceae: *Rhynchospora*
schomburgkiana; Orchidaceae: *Brachionidium longicaudatum*, *Crocodeilanthe moritzii*,
Epidendrum attenuatum, *Trichosalpinx* sp.; Dryopteridaceae: *Elaphoglossum*
paleaceum; Grammitidaceae: *Cochlidium attenuatum*, *C. furcatum*; Lycopodiaceae:
 365 *Lycopodium clavatum*). Six of the new summit records are from previously collected
 herbarium specimens that were not seen by treatment authors during the preparation of
 the FVG or were collected subsequent to its publication; these are *Elaphoglossum*
paleaceum, *Lycopodium clavatum*, *Mikania lucida* (Delascio Chitty, 1991), *Poa annua*
 and *Polypogon elongatus* (Delascio Chitty & Nozawa, 2010) and *Rhamnus ulei*. We did
 370 not locate 26 species that had been collected during previous expeditions.

Exotic species' richness

Among the 227 species recorded, we consider 13 to be exotics, representing 5.7% of the
 summit flora of Roraima. They are: *Gnaphalium elegans* and *Sonchus oleraceus*

(Asteraceae), *Rhynchospora schomburgkiana* and *Eleocharis filiculmis* (Cyperaceae),
Juncus effusus (Juncaceae), *Avenella flexuosa*, *Cinna poiformis*, *Poa annua*, *Polypogon*
elongatus and *Vulpia myuros* (Poaceae), *Rubus urticifolius* (Rosaceae), and
Lycopersicum esculentum and *Solanum tuberosum* (Solanaceae). With the exception of
Poa annua and *Polypogon elongatus*, which were recently reported at the Roraima
summit (Delascio Chitty & Nozawa, 2010), the rest of exotic species are here reported
as new records for the ETC summits. All of them have broad geographical distributions
outside of the Guayana Shield, with the exception of *Rhynchospora schomburgkiana*,
which heretofore was considered a lowland species (0--200 m elevation) from the upper
Rio Negro in Brazil, Venezuela and Colombia, and in Guyana. As shown in Figure 4,
the exotic species found atop the Roraima are distributed around camping areas, called
“hotels”.

Floristic composition, physiognomy, and phytogeography of the ETC summits

Based on current data, the richest summits of the ETC in terms of vascular plant
diversity are Roraima (227 species), Kukenán (137), and Ilú (128), followed by Yuruaní
(46), Maringma (40), Tramen (34), and Uei (33). Based on the number of new records
found on Roraima through intensive fieldwork, we expect the summit flora of all other
tepui to increase with further exploration. In particular, the flora of Karaurín may be
comprised of well over one hundred species, but it has only visited by botanists once
during a brief expedition in 1987, which yielded 14 species. To our knowledge no
botanical collections have been made on Wadakapiapué, Wei-Assipú, or Yakontipú.
However, photographs taken by herpetologists on the summit of Wei-Assipú (P. Kok,
personal communication) show a mosaic of exposed sandstone rock, mixed low
shrubby/herbaceous vegetation with at least the following species: *Bonnetia roraimae*,

Brocchinia reducta, *B. tatei*, *Epidendrum* sp., *Everardia* sp., *Microlicia benthamiana*,
Nietneria sp., *Orectanthe sceptrum*, *Connellia augustae*, *Heliamphora nutans*, *Racinaea*
spiculosa, *Stegolepis guianensis*, *Utricularia humboldtii*, and *Xyris* sp. Some taller
shrublands can be seen in more protected areas and are likely dominated by *Bonnetia*
(possibly *B. sessilis*).

Species richness on the ETC summits follows the same pattern as above within
the major vascular plant groups, Dicotyledonae, Monocotyledonae, and Pteridophyta
(Tables 3--5). Altogether, the ETC summits harbour at least 289 species (Online
Resource 1). As regards to Dicotyledonae, the summits of the ETC contain 31 families,
68 genera, and 122 species (Table 3). The richest families are Asteraceae (12 genera, 17
species), Ericaceae (8, 12), Melastomataceae (6, 11), and Rubiaceae (5, 10).

Monocotyledonae are represented by only 10 families, though these include large
numbers of genera and species (51, 93), especially Orchidaceae (17, 32) (Table 4).
Other rich families of monocots are Poaceae (12, 12), Cyperaceae (5, 12), Bromeliaceae
(5, 11), and Eriocaulaceae (5, 9). Finally, Pteridophyta are represented by 15 families,
32 genera, and 74 species (Table 5). Among the ETC summits, Pteridophyta are almost
exclusively known from only three tepuis, Roraima, Kukenán, and Ilú. Here, two
families stand out because of their high number of species: Grammitidaceae (7, 16) and
Dryopteridaceae (2, 10). Gymnospermae have not been found on any ETC summit.

However, we expect Podocarpaceae, particularly *Podocarpus roraimae* Pilg. to be
found on the lower, forested tepuis (e.g., Karaurín) as it has been collected at the base of
the wall on Roraima-tepui (*Steiermark 58949*, VEN) at approximately 2000--2350 m
elevation.

Endemic species richness and abundance of species of wide distribution among
the Neotropics increases as does total species richness in all biogeographic areas

considered for degree of endemism (Table 6). More than half of the species of the ETC
summits are endemic to the Guayana Shield (155, 53.6%), 100 to Pantepui (34.6%), 37
to the ETC (12.8%) and 10 to a single tepui (3.5%). The taxa with highest number of
Pantepui endemic species in the ETC are, for families: Orchidaceae (16), Asteraceae
(8), Ericaceae (6), and Rubiaceae (5), and for genera: *Epidendrum* (6), *Connellia* (3),
Cyathea (3, formerly *Hymenophyllopsis*, see Christenhusz, 2009), *Cybianthus* (3),
Paepalanthus (3), *Stegolepis* (3) and *Xyris* (3). There are no genera endemic to the ETC,
though *Connellia* (Bromeliaceae) appears to have a centre of diversity in the ETC with
three of its five species commonly found on most of the ETC summits. Both the number
of endemic species and degree of endemism is higher on Roraima than on other of the
ETC summits. The Roraima flora also has the highest percentage of exotic and the
highest percentage of widely distributed neotropical species, representing 5.7% and
44.9% of its summit vascular flora, respectively.

Three categories of growth forms were recognized among the ETC flora, namely
trees, shrubs, and herbs. Their corresponding physiognomic plant communities are low-
growing forests, shrublands, and meadows, with the latter divided into gramineous and
non-gramineous meadows. The ETC contains a total of 276 native species, distributed
in 183 herbaceous (66.3%), 82 shrubby (29.7%), and 11 forest species (4.0%).

Abundance of herbaceous and shrubby species is unequally distributed among the ETC
summits, as shown in Figure 5. Significant differences ($\chi^2 = 4.137$; $p = 0.042$) of the
abundance of herbs were found between Roraima, Kukenán, Ilú, Maringma, and
Tramen (average of 63.3% herbaceous species), and Yuruaní, Uei, and Karaurín
(42.9%). The latter three tepuis have similar percentages of herbaceous and shrubby
species. Relatively few species of trees are present on the ETC summits, with similar
abundances among tepuis, except for Karaurín, where no trees have been recorded.

We found a positive relationship between species richness and summit area at the scale of the ETC summits. Determination coefficients and significance of the relationship are given for log-log transformation of data: $r^2 = 0.640$; $p = 0.031$ with the total set of ETC species, and $r^2 = 0.516$; $p = 0.069$ using Pantepui endemics (Fig. 6). Finally, the analysis of floristic similarity based on Sørensen coefficients indicates a relatively high floristic affinity between the summits of Roraima and Kukenán (SSC = 0.69), Roraima and Ilú (SSC = 0.60), and Ilú and Kukenán (SSC = 0.62). Floristic similarity was relatively low for the remainder of tepui combinations.

Phytogeographic patterns in Pantepui

As depicted in Figure 7, 24 clusters of Pantepui endemic species were obtained. Their abundance and distribution indicate that the Pantepui endemic flora has very marked local distribution patterns. Districts are not grouped by endemic floras, rather the opposite; they have almost no endemic species in common. Despite that, some tepui clusters have been established based on their values of Raup-Crick floristic similarity. In the Eastern district, these groups are: 1) Roraima-Kukenán-Yuruaní, Karaurín-Ilú-Tramen, Uei, and Sierra de Lema; 2) Carrao-Ptarí, Los Testigos massif, Auyán massif, Uaipán, and Aprada; and 3) Chimantá massif and Angasima. In the Western district: 4) Guanay, Yaví, and Yutajé-Coro Coro; and 5) Cuao and Sipapo. In the Jaua-Duida district: 6) Jaua and Sarisariñama; and 7) Huachamacari, Duida, and Marahuaka. Noticeably, the updating and validation of the Pantepui database indicate that 17% of the Pantepui flora and 65% of the Pantepui endemic species are local endemics, that is, distributed over a single tepui or tepui massif.

Discussion

475 *Comparison of past-present-future botanical data*

Roraima is the tepui with the oldest botanical collections from its summit. In addition, it is probably the best known botanically due to the high number of expeditions (more than 50 since 1884), relative to the rest of tepuis. However, despite the abundant floristic information available on Roraima summit, an updated compilation has not been
 480 prepared since 1966 and that was based on field work carried out only through 1944 (Steyermark, 1966), long before any of the central or northern portions of the summit had been explored. Thus, we initiated a study of baseline diversity and endemism for future comparisons which included field and herbarium activities.

The Roraima summit is relatively small (34.4 km²) in comparison with other
 485 summit areas of Pantepui, which range from 200 to 500 km² (Huber, 1995a). This gives to the summit of Roraima certain advantages for repeated surveys for comparison with historical data, as it can serve, in a sense, as a permanent plot for vegetation monitoring, until homologated permanent plots can be installed (for example, 1 x 1 m quadrats required by GLORIA). However, some authors have questioned the applicability of
 490 historical plant records for comparative studies, due to uncertainties of their completeness and reproducibility (e.g., Vittoz *et al.*, 2008). According to Stöckli *et al.* (2011), historical data must meet two basic requirements. First, it must be reliable to be treated as presence/absence data (species not listed must be absent and not just unrecorded), and second, exact collection sites must be traceable. The second
 495 requirement may not be a major problem with the collections of Roraima. Although the oldest ones were not accompanied by geographical coordinates, collection areas may be delimited with certain confidence, thanks to the site descriptions made by collectors themselves in the labels of herbarium specimens or in expedition reports, and the difficulty in traversing the plateau by foot south to north.

500 Nevertheless, the first requirement may represent a limitation in the use of
historical data. In mountain ranges of temperate zones, the lower floristic diversity
(Nagy *et al.*, 2003), together with a longer and prolific botanical tradition (e.g., Stöckli
et al., 2011, in the Alps), suggest that many early twentieth century inventories are
reliable, therefore, that any new species subsequently found will not be the product of
505 incomplete previous inventories. This is neither the case of Pantepui nor of Roraima.
Indeed, the exploration of Pantepui still enables the discovery of species hitherto
unknown to specific places, as shown by the current 24% increase in species richness at
the Roraima summit through our surveys. This does not detract from historical data,
though. Comparative studies may use a representative sample of known species, for
510 example based on their ecological function, abundance, distribution, or biological
characteristics. Another possibility would be to use the total set of species, but then new
species records must be individually studied, identifying the processes that may have
led them to the summit, raising the corresponding hypothesis and seeking ways to test
them. Undoubtedly, this process involves more work and time, but is required to make
515 the most of such valuable data.

In the case of Roraima, four reasons emerge that can potentially explain the new
records: 1) upward climate-induced migration from lower altitudinal levels, 2) natural
migration processes, 3) intentional or unintentional translocation by humans and 4)
omissions in previous explorations. Except for hypothesis 4, where species would have
520 not moved at all (they were already present, but we did not know), the rest of
hypotheses involve range displacements. In hypotheses 1 and 2, species would have
arrived by their own means, whereas in hypothesis 3 they would have been transported
by humans. All three hypotheses may be tested by comparing past botanical collections
with the baseline of diversity and endemism established for the Roraima summit. For

example, some species were seen many times on southern slopes and base of walls, but not on the summit during historic expeditions, and have been repeatedly observed in the southern part of the summit during modern expeditions, indicating that they could have migrated from lower elevations (hypotheses 1 or 2). Specific knowledge of dispersal method and rates, local abundance and distance from the natural (previously known) range may be helpful to further differentiate each hypothetical case. Specifically, to disentangle hypotheses 1 and 2 a long-term monitoring of the species along an altitudinal transect, spanning from the base to the summit of Roraima, and establishing a record of the local climatic conditions, would provide the most accurate information to evaluate if there is an upward migration.

On Roraima, exotic species are found largely growing around camping sites (Fig. 4), which would suggest that humans have been the main vector. On the time scale of decades (the focus of invasive plant ecology), examples of exotic taxa introduced without associated human activities have been rare (but see Whittaker *et al.*, 1989). However, the high rates at which many plant taxa are being forced to move uphill due to ongoing global warming (1 to 5 m elev./yr) (Beckage *et al.*, 2008; Kelly & Goulden, 2008; Lenoir *et al.*, 2008) shows that, changes of geographical and/or elevational ranges due to non-direct human action may also occur at short time scales, thus suggesting the need for a case-by-case study of their characteristics in order to evaluate whether human actions or natural migration have been the effective cause of introduction. The following section describes our knowledge of the invasiveness characteristics and status in the tepui ecosystems (casual, naturalized, invasive) of each of the exotic species that we found on the Roraima summit, and hypothesizes their potential causes of introduction.

550 *Assessment of exotic species*

We consider the potato (*Solanum tuberosum*) and tomato (*Lycopersicum esculentum*), both Solanaceae, to be casual exotics. Cultivated plants are generally highly dependent on humans for their survival in wild conditions (Crawley *et al.*, 2001; Gepts & Papa, 2002). Therefore, we consider it unlikely that these two species will be able to further
555 propagate, except possibly for vegetative propagation of *Solanum tuberosum*. Additionally, the cultivated plants, especially those genetically modified, entail hybridization or introgression concerns with their wild relatives, conferring them characteristics such as resistance to herbivory by insects, fungi, etc. (Stewart *et al.*, 2003). However, the absence of native taxa of the Solanaceae family at the Roraima
560 summit discards this possibility.

Sonchus oleraceus (Asteraceae) is of European origin, though now widely considered as cosmopolitan (Aristeguieta, 1964). This is the first report of the genus for the Venezuelan Guayana, however, its presence was expected due to its widespread distribution and weedy nature (Pruski, 1997; Badillo *et al.*, 2008). The species is wind
565 dispersed by means of the feathery pappus on the fruit (achene), and reportedly the maximum dispersal distance of an individual plant is up to 7 m in controlled conditions (Sheldon & Burrows, 1973). According to Bullock & Clarke (2000), the maximum dispersal distance measured for a non-tree anemochoric plant is 80 m. Given that there were no previous reports of the species in the Guayana Shield, natural dispersal from
570 the nearest population seems unlikely so its introduction is probably due to human causes. It cannot be considered yet as naturalized because of the lack of previous reports and further its incipient colonies.

Gnaphalium elegans (Asteraceae) has a wide distribution among the Neotropics. In Venezuela, it mostly grows at the Coastal Range and the Andes (Pruski, 1997). As in

the case of *Sonchus oleraceus*, introduction by long-distance dispersal events may be uncommon given the large distance between the source populations and Pantepui. It is also found at high elevations on Sororopán-tepui, and Auyán-tepui, where it is reported to be abundant, but we consider these populations exotic as well, due to the limited wind dispersal capacity. In the Roraima summit, we documented it from a small population at a single hotel, which suggests human introduction and non-naturalized state.

Rhynchospora schomburgkiana (Cyperaceae) is naturally distributed in the lowlands of the Amazonas State of Venezuela, adjacent Colombia, Guyana, and northern Brazil (Thomas, 1998). Our collection from the summit of Roraima represents a significant change in the upper elevational range limit, from 200 to around 2700 m. We found it growing exclusively around the Roraima summit hotels, and suspect humans are the most probable cause of introduction. Pyšek *et al.* (2004) considered that, for exotic species to be considered naturalized, a 10-year period of persistence at a site may be required, which would reflect possible negative effects of short-term ‘catastrophic events’ (e.g., climatic extremes, outbreak of pests and pathogens). Despite the lack of previous reports, we believe that, for conservation purposes, this viviparous species found growing around numerous hotels on the Venezuelan side, should be considered as naturalized on Roraima.

Eleocharis filiculmis (Cyperaceae) is the most widespread species of the genus in the Venezuelan Guayana. However, prior to our surveys it was not known to exceed 1400 m elevation (González-Elizondo & Reznicek, 1998). Its presence on the Roraima summit is likely due to human causes, as it was only found growing in the vicinity of a hotel. It cannot be considered naturalized.

Juncus effusus (Juncaceae) is a cosmopolitan species, common in northern temperate regions and found at high elevation of the tropics (Balslev, 1996). In Venezuela, it is known to be a species of the cool highlands of the Andes and the Coastal Range. On Roraima, it was observed forming small colonies at disturbed camp areas and their surroundings; as such, we postulate its presence is due to human activities. Its status in the ecosystem is not easy to establish, given the lack of previous reports. However, its presence in two hotels (being the population of Hotel Basilio particularly vigorous), together with its rhizomatous nature and its consequent potential for vegetative reproduction, suggest it to be treated, at least for conservation purposes, as naturalized.

Rubus urticifolius (Rosaceae) was widely reported on the slopes of Roraima by many collectors (e.g., Im Thurn, 1885), but never on the summit. Though our collection is the first known record of the species on the summit, we consider it fully naturalized given the presence of spiny thickets many meters in diameter at several hotels. In addition, the records from the slopes suggest that the species will be able to survive and reproduce consistently on the summit. This species produces drupelet-like fruits which are eaten and dispersed by birds (Rincón, 2005), while other species of the genus showing similar fruits are dispersed by mammals as well (Brunner *et al.*, 1976; Fedriani & Delibes, 2009). The populations of the Roraima summit may have been transported either by the mammals (coatis) or birds reported for the zone. However, it is worth noting that many of them were located around hotels, thus suggesting that the species was carried to the summit by humans from populations on the slopes.

We found five species of Poaceae in as many genera growing widely around the hotels, all of which are considered exotic to the Venezuelan Guayana. *Avenella* (*Deschampsia*) is a new genus record for Venezuela and *Cinna* and *Vulpia* are new

genus records for the Venezuelan Guayana. *Poa annua* and *Polypogon elongatus* were
625 previously reported to occur on the Roraima summit by Delascio Chitty & Nozawa
(2010). The first three mentioned were found only around hotels and were possibly
introduced by humans. They cannot yet be considered naturalized due to the lack of
historic records from the area and the small number of individuals seen. However,
Avenella flexuosa is of concern because of its pseudo-viviparous reproduction, a
630 mechanism that allows the generation of progeny without crossing. To our knowledge
this is the first report of pseudo-vivipary in this species.

In its natural range, *Avenella flexuosa* commonly grows below 1000 m elevation
in all continents, including Argentina and Chile in South America (Cialdella & Zuloaga,
2010). However, we found it around 2700 m elevation, which coincides with a similar
635 report from Costa Rica at nearly 3000 m elevation (Davidse & Pohl, 1994). In the case
of *Cinna poiformis*, it is distributed from Mexico to Bolivia (Brandenburg *et al.*, 1991).
In Venezuela, it is known from cool regions of the Andes and the Coastal Range. On
Roraima, we found several clumps in different spaces of the same hotel. Finally, *Vulpia*
myuros is native to Europe and Northern Africa (Lonard, 2007).

640 Both *Poa annua* and *Polypogon elongatus* are distributed naturally in cool
regions of the Andes and the Coastal Range. *Poa annua* is an introduced and naturalized
species in the New World (Soreng *et al.*, 2003), whereas *Polypogon elongatus* has an
American origin, growing from southern U.S.A. to Argentina. *Poa annua* was first
reported as possibly occurring on the summit in 2002 (Davidse *et al.*, 2004) and the first
645 herbarium vouchers for both species were reported in 2008 (Delascio Chitty & Nozawa,
2010). At present, both species have relatively extensive populations and are present
around almost all hotels. *Polypogon elongatus* has exceeded the dispersion rate
suggested by Richardson *et al.* (2000) and Pyšek *et al.* (2004) to be considered invasive

(>100 m from parent plants in <50 years) and *Poa annua* will likely do the same in the next few years if no management actions are undertaken. Both are well-known invasive plants (Schroeder *et al.*, 1993; Holm *et al.*, 1997), with *Poa annua* already recognized as such in Venezuela (Ojasti, 2001). Therefore, we consider them to be invasive or potentially invasive on Roraima, following the Precautionary Principle (Cooney, 2004). Fortunately, neither has been found in undisturbed areas of the summit.

In summary, as almost all of the exotic species are new reports for the ETC, the nearest populations, which are found hundreds of kilometres away, should have suffered long-distance dispersal events to reach the Roraima summit in a natural way. According to Cain *et al.* (2000), these can be achieved through wind (anemochory), water (hydrochory) or vertebrates (zoochory) dispersal. Hydrochory would not seem to be an option given the >2700 m elevation at which the Roraima summit is found, and long-distance dispersal by wind would not seem to be as common as previously thought (Bullock & Clarke, 2000; Renner, 2004). In depth studies would be required to reach sound conclusions about dispersal agent, and population genetics may help to establish the relationships between the populations of the Roraima summit and the neighbouring ones. At the moment, all the available data points towards a human-mediated introduction of these species.

Floristic and physiognomic patterns of the ETC summits

Table 7 summarizes the taxonomic richness by traditional major groups (gymnosperms, angiosperms, and pteridophytes) in different biogeographic units, namely the Roraima summit, the ETC summits, Pantepui, and the Venezuelan Guayana. All of them exhibit a higher diversity of angiosperms (A) than of pteridophytes (P). The ratio A/P increases as does the area of the biogeographic units considered, which suggests that the tepui

summits, and especially the ones with patches of vegetation and rocky habitats like

675 Roraima, are comparatively more prone to harbour higher diversity of pteridophyte
 species. As for gymnosperms, the Venezuelan Guayana has relatively little diversity
 overall, with only three native families, each one represented by a single genus:
 Gnetaceae (*Gnetum*: 7 spp.), Podocarpaceae (*Podocarpus*: 10 spp.), and Zamiaceae,
 (Zamia: 4 spp.) (Hokche *et al.*, 2008). Together they account for just 21 species. This
 680 level of diversity is similar to that of Peru and the Guianas, with 17 species in four
 families native to Peru (Brako & Zarucchi, 1993), and only four species in two families
 native to the Guianas (Boggan *et al.*, 1992). However, both *Gnetum* and *Podocarpus* are
 known widely from other tepuis and tepui slopes ranging up to 1800 m and 2700 m
 respectively, and quite possible will be found in the ETC.

685 At the ETC level, the available information points towards a higher species
 richness on Roraima, Kukenán, and Ilú. Nogué *et al.* (2009), applying the species-area
 relationship to the area of Pantepui at 100 m elevation intervals, and Riina (2003), using
 tepui summit areas, proved that a significant positive relationship existed between area
 and species richness in Pantepui. Our data also support this relationship at the scale of
 690 the ETC summits (Fig. 6), on the understanding that a wider botanical knowledge of the
 ETC summits as a whole may introduce some variation in the patterns of species
 richness and endemism derived from the currently available data. In addition, local
 endemism at species level on the summit of Roraima (2 species, 0.9%) (Table 6) is
 much lower than that previously proposed by Gleason (68--90%; Gleason, 1929) or
 695 Steyermark (54%; Steyermark, 1966). These high estimates were the result of
 incomplete knowledge of tepui species distribution at the time, and we expect further
 exploration on summits and slopes to yield lower levels of endemism than currently
 believed for other tepuis as well.

Distribution and abundance of the three growth forms (herbs, shrubs, and trees)

700 show differences among the ETC tepuis, which may be explained by the tepui morphology and the ecological requirements of each vegetation type. The dwarf, evergreen, high-tepui forests and shrublands grow commonly in organic soils (histosols) of black peat overlying sandstone, which are generally restricted to wind-protected sites or depressions (Huber, 1995b). Soil availability, its nutrient content, wind, and solar
705 radiation are thus the main factors limiting the distribution of these plant formations atop the rocky summits of the ETC. Herbaceous vegetation types dominated by grasses and/or sedges (Poaceae and Cyperaceae) occur sporadically in upper montane localities of Pantepui (Huber, 1995b). On the ETC, they clearly play a secondary role in most of the herbaceous plant communities, although they can be successful under some
710 particular site conditions, for example, in periodically water-logged areas of peat located in wide valley bottoms, as in the case of *Cladium costatum* (Cyperaceae) and of *Cortaderia roraimensis* (Poaceae) on Roraima. Non-gramineous meadows are very characteristic of the vegetation of the Venezuelan Guayana. In the highlands, species of Rapateaceae, an entirely herbaceous monocot family, have reached a great degree of
715 differentiation and predominate in the herb layer (Huber, 1995b, 2006). On the rocky, open, and windswept plateaus of Roraima, Kukenán, Yuruaní, Ilú, and Tramen, meadows are distributed in small patches of herbaceous and subshrubby species growing preferably on shallow to deep, extremely acidic and water-saturated organic soils, although in some cases they may be found growing on rocky substrates,
720 performing as pioneer species (Huber, 2006). The herbaceous vegetation on Uei is notably different from that of the rest of tepuis of the ETC, as it contains different floristic composition and soil characteristics; its summit is covered by a relatively thick brown soil which is absent in the other tepuis (Huber, 2006). In addition, Uei is

separated from the remaining tepui chain by a distance 20 km, whereas the remaining
725 tepuis are separated from one another by distances of 1--9 km.

Based on the vegetation descriptions of Huber (1995*b*, 2006), six tepuis
(Tramen, Ilú, Yuruaní, Kukenán, Roraima, and Wei-Assipú) have rocky summits with
herbaceous vegetation along with patches of shrub or elfin forest in protected places,
whereas the rest (Karaurín, Wadakapiapué, Yakontipú, Maringma, and Uei) are
730 completely covered with a combination of shrublands and tepui meadows. This pattern
is well reflected in the analysis of growth forms depicted in Figure 5. The only
discrepancies in our results with respect to the patterns described above are the
relatively low abundance of shrubs on Maringma, showing a distribution of growth
forms similar to the rocky plateaus, and the predominance of shrubs over meadows in
735 Yuruaní, a tepui with a rocky summit that shares most features with Roraima and
Kukenán. For the moment, these facts may not be resolved with the available data.
Potential changes in the composition of the mentioned tepui communities atop the ETC
summits, associated to individual responses to climate change, may be detected by
comparing present and future relative abundances of species with different growth
740 forms, or alternatively by measuring the cover of each physiognomic type on a regular
basis, either directly on the ground or through the analysis of aerial photographs.

Phytogeographic patterns

According to our results, Pantepui shows a high degree of endemism, with many plant
745 species being local endemics. This characteristic of the Pantepui flora has attracted the
attention of many researchers, though most of them formed their hypotheses using
present-day botanical and phytogeographical studies (see Rull, 2004*a*). To date the only
model using evidence of the past that attempted to explain the biogeographic patterns of

Pantepui and the origin of its high endemism of vascular plants was based on

750 Quaternary glacial/interglacial cycles, assuming that species shifted proportionally to temperature changes. One-hundred and three cold and warm stages have alternated since the beginning of the Quaternary 2.588 Ma, with a frequency of 41,000 years until 1 Ma, and 100,000 years after that (Lisiecki & Raymo, 2005). On the top of the tepuis, it is likely that open ground predominated even during glaciations, as no geologic or
755 geomorphologic feature demonstrating the presence of past ice sheets has ever been documented. According to the above-mentioned model, downward migration of species during glacial phases promoted sympatric speciation, hybridization, and polyploidy, whereas vicariance occurred during interglacials, when species moved upwards. This would have resulted in a net increase of diversity and endemism favoured by the
760 complex topography and habitat heterogeneity of Pantepui (Rull, 2004a, 2004b, 2004c, 2005). It is worth noting that the role of Quaternary climatic cycles in neotropical diversification has been already stated in several phylogeographic studies (e.g., Richardson *et al.*, 2001; Givnish *et al.*, 2004, 2011; Noonan & Gaucher, 2005, 2006). On this basis, Rull & Nogué (2007) conducted a detailed physiographical study to
765 reconstruct the potential migration routes and barriers of the Quaternary in Pantepui and found that a significant 40% (164 species) of present high-altitude local endemics were unable to migrate, even during glaciations when temperatures in the Neotropics were about 5--6 °C lower than today (Farrera *et al.*, 1999, for the last glacial maximum, 21,000 years BP). In other words, 81% of the isolated flora (unable to migrate even
770 during glacial maxima) is comprised of local endemics. Indeed, our results show a high percentage of agreement with the hypothesis of migratory routes and barriers suggested by these authors.

For example, the disappearance of temperature-induced barriers to migration for vascular plants among the four districts occurred when species moved down 900 m below their current ranges, so that only the species with current lower altitudinal distribution level below 1700 m could take advantage of the migration pathways for gene flow among districts. Therefore, the magnitude of the potential genetic interchange between highland and lowland species throughout the different districts of Pantepui must have been quite limited, thus explaining their high present-day floristic differentiation, especially concerning Pantepui endemics (Fig. 7). As regards to the ETC, the tepuis that comprise it kept their migratory routes opened during most of the Quaternary (Nogué & Rull, 2007); a barrier between Roraima-Kukenán-Yuruaní and Karaurín-Ilú-Tramen only appeared when temperature increased such that the difference with respect to the present one was lower than 1.6 °C. The maintenance of migratory routes between these two groups of tepuis, together with their geographic proximity, may have defined their present-day similar composition of endemics. Uei-tepui, for its part, has gradual slopes for the most part that connect the summit to the surrounding lowlands, and as mentioned is relatively isolated from the rest of the tepuis of the ETC. This may explain the low number of Pantepui endemics on its summit (4) and the floristic differentiation with respect to the neighbouring tepuis. The Guaiquinima massif, a large massif of 1096 km² and 1650 m elevation, is one of the most dissimilar tepuis in terms of floristic composition. This may be due to its geographic isolation from the rest of tepuis, with marked valleys in between (Vegas-Vilarrúbia *et al.*, 2012), and the fact that its summit is connected to the Gran Sabana lowlands, and is mainly covered by upland forest species; only a portion of 50 m² of its summit belongs to the high-tepui biome.

Overall, local endemism in Pantepui have more weight than endemism at Pantepui level. The percentage of local endemism obtained for Pantepui (17%) strongly supports the vision of Pantepui as a continental archipelago (Rull, 2010). Indeed, the island/archipelago pattern of endemism in Pantepui is similar to those of oceanic islands, as supported by its proportion of endemic species (30% Pantepui endemics) in comparison with other islands such as the Galápagos (40%), Cape Verde (30%), Jamaica (27%), or Seychelles (15%) (Whittaker & Fernández-Palacios, 2007). We suggest that patterns of vascular plant diversity and endemism in Pantepui should be ideally studied using island biogeography techniques. Recently, species-area relationships were applied to the Pantepui flora to estimate biodiversity loss through potential habitat loss by global warming (Nogué *et al.*, 2009). Another possibility would be to analyse nestedness patterns (Patterson & Atmar, 1986), which has been mostly applied to studies on insular archipelagos (Wright *et al.*, 1998 and literature therein) and which could have implications on the conservation of the Pantepui biome. For example, nestedness indexes may inform the decision of whether single large conservation areas are more effective in preserving biodiversity than several small areas. A strong degree of richness-ordered nestedness (where data matrix is ordered by the size of the flora or fauna) would imply that most species could be represented by conserving the richest (largest) patch. Conversely, a low degree of nestedness would mean that particular habitat patches contain different species sets and that several reserves of differing size and richness may be required to maximize regional diversity (Whittaker & Fernández-Palacios, 2007). In this regard, Vegas-Vilarrúbia *et al.* (2012) suggested the Chimantá massif as a potential refugium for the Pantepui flora, due to the possible large remaining habitat (43%) after the 4 °C temperature increase forecast for the area by the end of this century by the A2 IPCC scenario. The analysis of distributional patterns of the Pantepui

endemic flora may provide additional criteria to support or readjust the recommendations derived from the study of Vegas-Vilarrúbia *et al.* (2012).

As regards to the ETC, summit area explains quite well the differences in species richness on the ETC summits (Fig. 6). However, the study of the phytogeographical patterns of the ETC, as well as of Pantepui, would greatly benefit from a multivariate direct gradient analysis, which deal simultaneously with species and many environmental variables (Jongman *et al.*, 1995; Quinn & Keough, 2002). For the moment, elevation and summit area are the only ones readily available. We carried out a preliminary Detrended Canonical Correspondence Analysis (DCCA) with these two variables and the ETC summit species but it did not provide much novel information. Therefore, a better understanding may be developed by analysing additional factors, such as soil and microclimate. Additionally, information about dispersal mechanisms is still largely unknown for the native Pantepui plant species, thus preventing the estimation of a more realistic dispersal capacity and migration rates. DNA-based phylogeographical studies are also lacking, which would significantly improve our understanding of the present-day biogeographic, richness, and endemism patterns of the Pantepui flora.

Conservation opportunities

Tourism activities throughout Pantepui have increased in recent decades, in parallel with the decrease of scientific expeditions (Rull, 2010). Unfortunately, the effects of tourism were markedly evident on the Roraima summit during our visits, increasing noticeably even from 2011 to 2012, especially the trampling of vegetation. Effects of such trampling on tepuis, even without recurrence may take longer than several decades to recover (Gorzula & Huber, 1992). As well, we noticed the presence of garbage, food

scraps, toilet paper, human excrement, graffiti, and abundant exotic species around camping areas, as well as mining equipment found sequestered away from the camps. Invasive plants may have the potential to reduce fitness of native species by reducing
850 their populations, while overcoming the environmental barriers imposed by acidic and poorly developed soils, limited nutrient availability and high solar radiation. Therefore, given the remarkable diversity, endemism, and uniqueness of the tepui flora (Berry *et al.*, 1995; Huber, 1995b), the tourism impacts discovered during this study on the Roraima summit have major implications for tourism management and conservation of
855 the Pantepui flora as a whole.

In accordance with the Venezuelan National Strategy 2010-2020 for the Conservation of Biodiversity (MINAMB, 2010), we recommend that management of exotic species on Roraima be based on four strategies: 1) prevention of new introductions, 2) early detection of new populations, 3) monitoring of existing
860 populations, and 4) containment or eradication of the most aggressive species. To prevent the arrival of new propagules, vectors and introduction pathways need to be evaluated to determine their level of introduction potential. In this regard, proximity of the exotic species to hotels (Fig. 4) suggests that propagules are transported by humans. Unlike lowland areas where arrival/departure points may be numerous, tepui summits
865 have very few points of access, which means that preventive actions could be focused. In the case of Roraima, ascent to the summit is largely by foot. Lesser visitation is by helicopter, though with typically lesser levels of oversight. Cooperation of park managers and tourist guides at an early stage is essential in raising awareness among tourists. Surveys to detect new populations and the monitoring of the existing ones
870 should be conducted on a regular basis, especially of the camp surroundings. Any control action upon exotic populations should be subjected to an environmental impact

assessment (Erickson, 1994), and to a prioritization of the significance of their potential impact and feasibility of controlling or managing their populations (e.g., Hiebert & Stubbendieck, 1993; Brunel *et al.*, 2010).

875 The majority of the Roraima exotics may be easy to eradicate because of the low number of individuals and the restricted areas of distribution. However, eradication of *Rhynchospora schomburgkiana* and *Polypogon elongatus* may be more difficult. *Rhynchospora schomburgkiana* is an herb of short stature which can be easily pulled from the soil. Yet, the same short stature makes it inconspicuous and small clumps may
 880 escape the human eye. The goal for *Polypogon elongatus* should also be the containment of its population. Nevertheless, there are two incipient populations for which we recommend eradication. The first one is at Hotel Coatí, represented by a few sparse clumps, and the second is located far from the camps along the pathway to the ‘Jacuzzis’. Populations at the remaining hotels should be contained or eliminated,
 885 particularly those at the Hotel Indio, which appear to be especially vigorous. Based on our observations and using the framework proposed by Hiebert & Stubbendieck (1993), we provide a preliminary prioritization of control actions in Figure 8.

 Overall, existing knowledge of these species and their invasiveness, although limited, should be enough to start controlling proactively their populations, for various
 890 reasons. Firstly, prompt implementation of eradication actions, that is, when number of individuals is low and the species is still in the naturalized phase, normally leads to better outcomes (McNeely *et al.*, 2001). In this regard, time lag for tropical plant invasions may be much shorter than previously thought (5 and 14 years for herbaceous and woody plants, respectively) (Daehler, 2009). Secondly, the rugged terrain and
 895 remoteness of Roraima summit may make containment and eradication especially costly and difficult; and finally, the autochthonous flora of the Roraima summit is composed

of many endemic species, which are in turn threatened by potential climate-induced habitat fragmentation and/or loss, and the possible migration to higher elevations of competitors and pathogens. Indeed, potential synergies between human-mediated
900 invasions and climate change could produce non-linear, mutually reinforcing ecological responses (Brook *et al.*, 2008; Walther *et al.*, 2009 and literature therein), which in our case may radically change the diversity and endemism patterns on the tepui summits, as well as the composition of their unique communities. In view of these forecasts, a permanent monitoring site assessing the response of native and non-native tepui flora to
905 climate change could be implemented since, to our knowledge, very few studies have addressed this issue in flat-topped and vegetated mountain summits (but see Kreyling *et al.*, 2010). In this context, the Roraima summit should be conceived as a pilot study to assess the possibility of adhesion to GLORIA. At the moment, the option of monitoring plots is being considered for all Pantepui. An equally interesting and desirable option
910 would be to establish and monitor the upper and lower limits of distribution in Roraima of some of its keystone species, but the incomplete floristic knowledge of vegetation growing on its slopes represents a significant limitation. Finally, in order to investigate the tolerance thresholds and estimate the time lag to the forecasted climatic changes, it would be recommendable to establish an envelope of tolerance to combined variations
915 of abiotic factors in laboratory experiments for the keystone or most endangered species, according to the priority categories previously established by Safont *et al.* (2012). Hence, Roraima has great potential as a natural laboratory where the hypothesis of upward migration and local extinctions may be tested (Rull, 2010), and also offers to scientists and land-managers the opportunity to respond in time to preserve its unique
920 flora from both climate change and human impacts.

Conclusions

The only information currently available for Pantepui concerning plant responses to climate change comes from models based on IPCC projections, which predict high habitat loss by the end of this century associated with significant plant diversity declines on many tepuis (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al.*, 2009; Safont *et al.*, 2012; Vegas-Vilarrúbia *et al.*, 2012). Our inventory establishes a baseline of diversity and endemism on the Roraima summit, which can be compared with past historical plant surveys and herbarium records (dating back to 1884). This, along with future surveys can help verify whether or not species migrate or become extinct due to climate change. Roraima-tepui is especially suited for comparative studies on the effect of climate change on plant diversity as it harbours a good representation of the flora of Pantepui and because of its long history of botanical collections.

The Roraima summit flora is comprised of 227 known vascular plant species, 42 of which are added to the summit flora as a result of this study, and two others from works published after the completion of the FVG. One of the species, belonging to the genus *Epidendrum* (Orchidaceae), has been confirmed to be new for science. The inventory also confirmed the existence of 13 exotic species, most likely transported by humans, among which *Poa annua* and *Polypogon elongatus* (Poaceae) are noteworthy due to their invasive potential.

At the present state of botanical exploration, Roraima appears to be the tepui of the ETC with the highest species richness and degree of endemism. The tepuis showing the highest floristic similarity are Roraima, Kukenán, and Ilú. These tepuis, together with Tramen and Maringma, show a dominance of herbaceous species over shrubs, whereas Yuruaní, Karaurín, and Uei reach similar abundances. The only discrepancies in our results with respect to vegetation descriptions of Huber (1995b, 2006) are the

relatively low abundance of shrubs on Maringma, and the predominance of shrubs over meadows in Yuruaní. For the moment, these facts may not be resolved with the available data. Furthermore, we found a significant positive relationship between total species richness and summit area at the scale of the ETC, a result which agrees with the pattern found in Pantepui by Riina (2003) and Nogué *et al.* (2009).

The endemic flora of Pantepui shows very marked local distribution patterns. These patterns are in accordance with hypothesized location and timing of appearance and disappearance of migratory routes in Pantepui during the climatic cycles of the Quaternary (Rull & Nogué, 2007). Our results show that 17% of the Pantepui species and 65% of the Pantepui endemic species are local endemics. Given the archipelago-like pattern of endemism prevailing in Pantepui, the use of island biogeography techniques are recommended to further study floristic patterns.

As for future research, both species and community-level changes taking place at the Roraima summit in the coming decades may be evaluated through the implementation of an integrated monitoring program, including measures of local climate, soil, and vegetation. Although our work focused on a single tepui, results of long-term monitoring on the Roraima summit would be relevant to the whole Pantepui province, and also to the Neotropics, as Pantepui is one of its most diverse and endemic biomes (Berry *et al.*, 1995).

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1325 **Tables**

Table 1. Tepuis of the ETC, indicating the countries to which they belong, the elevation and the summit area. Sources: The Survey Department of Guyana (1975); Huber (1995a); Kok (2009); B. Holst (unpublished data derived from Google Earth Pro).

| Tepui | Country | Elevation (m) | Summit area (km ²) |
|-------------------|---------------------------|-------------------|--------------------------------|
| Uei – Ue | Venezuela, Brazil | 2250 | 2.5 |
| Maringma – Mr | Brazil, Guyana | 2150 | 1.3 ^a |
| Yakontipú – Yk | Brazil, Guyana | 2320 ^a | 0.5 ^a |
| Wei-Assipú – We | Brazil, Guyana | 2280 | 1.5 ^a |
| Roraima – Ro | Venezuela, Brazil, Guyana | 2810 | 34.4 |
| Kukenán – Kn | Venezuela | 2650 | 20.6 |
| Yuruaní – Yu | Venezuela | 2300 | 4.4 |
| Wadakapiapué – Wp | Venezuela | 2000 | <0.01 |
| Karaurín – Kr | Venezuela | 2450 | 1.9 |
| Ilú – Il | Venezuela | 2700 | 4.7 ^a |
| Tramen – Tr | Venezuela | 2700 | 0.1 ^a |
| Total ETC | | | 71.9 |

1330 ^a Estimated from Google Earth Pro.

Table 2. Most diverse families and genera of the Roraima summit.

| Family | Genera | Species | Genus | Species |
|-----------------|--------|---------|--|---------|
| Orchidaceae | 15 | 26 | <i>Elaphoglossum</i> (Dryopteridaceae) | 8 |
| Grammitidaceae | 7 | 16 | <i>Epidendrum</i> (Orchidaceae) | 7 |
| Asteraceae | 10 | 13 | <i>Xyris</i> (Xyridaceae) | 6 |
| Cyperaceae | 5 | 11 | <i>Octomeria</i> (Orchidaceae) | 5 |
| Bromeliaceae | 5 | 10 | <i>Peperomia</i> (Piperaceae) | 5 |
| Dryopteridaceae | 2 | 10 | <i>Pterozonium</i> (Pteridaceae) | 5 |
| Poaceae | 9 | 9 | <i>Utricularia</i> (Lentibulariaceae) | 5 |
| Ericaceae | 7 | 9 | Total | 41 |
| Pteridaceae | 2 | 8 | | |
| Total | 62 | 112 | | |

Table 3. Richness of Dicotyledonae on the ETC summits (number of genera/number of species). Tepuis are grouped according to species

richness.

Dicotyledonae (here including Magnoliids and Eudicots)

| | Apocynaceae | Aquifoliaceae | Araliaceae | Asteraceae | Bonnetiaceae | Clusiaceae | Cunoniaceae | Cyrillaceae | Droseraceae | Ericaceae | Gentianaceae | Hypericaceae | Lentibulariaceae | Melastomataceae | Myrsinaceae | Myrtaceae | Ochnaceae | Passifloraceae | Phyllanthaceae | Piperaceae | Polygalaceae | Polygonaceae | Rhamnaceae | Rosaceae | Rubiaceae | Santalaceae | Sarraceniaceae | Scrophulariaceae | Solanaceae | Symplocaceae | Winteraceae | Total |
|-----------|-------------|---------------|------------|------------|--------------|------------|-------------|-------------|-------------|-----------|--------------|--------------|------------------|-----------------|-------------|-----------|-----------|----------------|----------------|------------|--------------|--------------|------------|----------|-----------|-------------|----------------|------------------|------------|--------------|-------------|--------|
| Roraima | 1/2 | 1/3 | 1/2 | 10/13 | 1/1 | - | 1/4 | 1/1 | 1/2 | 7/9 | 3/3 | 1/1 | 2/7 | 5/7 | 2/2 | 1/1 | 1/1 | - | - | 1/5 | 1/1 | - | 1/1 | 2/2 | 4/6 | 1/2 | 1/1 | - | 2/2 | 1/1 | 1/1 | 54/81 |
| Kukenán | 1/1 | 1/2 | 1/2 | 7/8 | 1/1 | 1/1 | 1/3 | 1/1 | 1/1 | 8/10 | 3/3 | 1/1 | 2/8 | 2/3 | 2/3 | 1/1 | 1/1 | - | - | 1/1 | - | - | - | - | 4/4 | 1/2 | 1/1 | - | - | - | 1/1 | 43/58 |
| Ilú | 1/1 | 1/2 | 1/2 | 6/8 | 1/1 | 1/1 | 1/4 | 1/1 | 1/1 | 7/9 | 3/3 | - | 2/4 | 4/6 | 2/4 | 2/2 | 2/2 | - | - | 1/4 | - | 1/1 | - | 1/1 | 4/6 | 1/2 | 1/4 | 1/1 | - | - | 1/1 | 47/71 |
| Yuruaní | - | 1/1 | 1/2 | 4/4 | 1/2 | - | 1/1 | 1/1 | 1/1 | 4/4 | - | - | 1/2 | 2/2 | 1/2 | 1/1 | 2/2 | - | - | - | - | - | - | - | 3/4 | - | 1/2 | - | - | - | - | 25/31 |
| Maringma | - | 1/1 | 1/1 | 2/2 | 1/1 | 1/1 | - | 1/1 | 1/3 | 1/1 | - | - | 1/1 | 2/2 | 1/1 | 1/1 | 2/2 | - | - | - | - | - | - | - | 3/3 | - | 1/1 | - | - | - | - | 20/22 |
| Tramen | - | - | - | 1/1 | 1/1 | - | 1/1 | 1/1 | 1/1 | 2/3 | 1/1 | - | 1/1 | 3/3 | - | 1/1 | 1/1 | - | - | - | - | - | - | - | - | - | 1/2 | - | - | - | - | 15/17 |
| Uei | - | - | - | 4/4 | 1/1 | 2/2 | - | 1/1 | - | 2/2 | - | - | 1/1 | 4/4 | 1/1 | - | - | 1/1 | 1/1 | - | 1/1 | 1/1 | - | - | - | - | 1/1 | - | - | - | - | 21/21 |
| Karaurín | - | - | - | 2/2 | - | - | - | 1/1 | 1/1 | 1/1 | - | - | - | - | - | 1/1 | 2/2 | - | - | - | - | - | - | - | 1/1 | - | 1/1 | - | - | - | - | 10/10 |
| Total ETC | 1/2 | 1/3 | 1/2 | 12/17 | 1/2 | 2/2 | 1/6 | 1/1 | 1/4 | 8/12 | 3/4 | 1/1 | 2/10 | 6/11 | 2/7 | 2/2 | 3/3 | 1/1 | 1/1 | 1/5 | 1/1 | 1/1 | 1/1 | 2/2 | 5/10 | 1/2 | 1/4 | 1/1 | 2/2 | 1/1 | 1/1 | 68/122 |

Table 4. Richness of Monocotyledonae on the ETC summits (number of genera/number of species). Tepuis are grouped according to species richness.

| Monocotyledonae | | | | | | | | | | | |
|-----------------|--------------|------------|---------------|-----------|---------------|-------------|---------|-------------|---------------|------------|-------|
| | Bromeliaceae | Cyperaceae | Eriocaulaceae | Juncaceae | Nartheciaceae | Orchidaceae | Poaceae | Rapateaceae | Tofieldiaceae | Xyridaceae | Total |
| Roraima | 5/10 | 5/11 | 5/7 | 1/1 | 1/2 | 15/26 | 9/9 | 1/2 | 1/1 | 2/7 | 45/76 |
| Kukenán | 5/7 | 2/3 | 5/5 | - | 1/1 | 14/21 | 2/2 | 1/2 | 1/1 | 2/7 | 33/49 |
| Ilú | 2/3 | 3/5 | 4/6 | - | - | 8/12 | 3/3 | 1/1 | - | 2/4 | 23/34 |
| Yuruaní | 1/2 | - | 3/3 | - | 1/1 | 2/2 | 1/1 | 1/1 | 1/1 | 1/2 | 11/13 |
| Maringma | 4/4 | 2/2 | 1/1 | - | - | - | 1/1 | 1/2 | 1/1 | 3/4 | 13/15 |
| Tramen | 2/2 | 2/3 | 1/1 | - | - | 2/3 | 1/1 | 1/1 | 1/1 | 1/1 | 11/13 |
| Uei | 1/1 | 1/1 | 3/3 | - | - | 1/1 | 2/2 | 1/1 | - | 2/2 | 11/11 |
| Kaurín | - | 1/1 | 1/1 | - | - | - | 1/1 | 1/1 | - | - | 4/4 |
| Total ETC | 5/11 | 5/12 | 5/9 | 1/1 | 1/2 | 17/32 | 12/12 | 1/3 | 1/1 | 3/10 | 51/93 |

Table 5. Richness of Pteridophyta on the ETC summits (number of genera/number of species). Tepuis are grouped according to species richness.

| Pteridophyta | | | | | | | | | | | | | | | | |
|--------------|--------------|-------------|-------------|------------------|---------------|-----------------|----------------|----------------|------------------|------------|---------------|---------------|-------------|-----------------|------------------|-------|
| | Aspleniaceae | Blechnaceae | Cyatheaceae | Dennstaedtiaceae | Dicksoniaceae | Dryopteridaceae | Gleicheniaceae | Grammitidaceae | Hymenophyllaceae | Isoetaceae | Lycopodiaceae | Polypodiaceae | Pteridaceae | Selaginellaceae | Thelypteridaceae | Total |
| Roraima | 1/2 | 1/3 | 1/4 | 5/5 | 1/1 | 2/10 | 2/3 | 7/16 | 2/6 | 1/1 | 3/5 | 1/1 | 2/8 | 1/3 | 1/2 | 31/70 |
| Kukenán | 1/1 | 1/1 | 1/3 | 1/1 | - | 2/3 | 1/1 | 6/8 | 1/2 | - | 2/4 | - | 2/4 | 1/2 | - | 19/30 |
| Ilú | 1/1 | 1/1 | 1/3 | 1/1 | - | 1/1 | 1/1 | 4/5 | 1/1 | 1/1 | 2/2 | - | 2/4 | 1/1 | 1/1 | 18/23 |
| Yuruaní | - | - | - | - | - | - | - | - | - | - | 1/1 | - | 1/1 | - | - | 2/2 |
| Maringma | - | - | - | 1/1 | - | - | - | - | - | - | 1/1 | 1/1 | - | - | - | 3/3 |
| Tramen | 1/1 | - | 1/1 | - | - | 1/1 | - | - | - | - | - | - | 1/1 | - | - | 4/4 |
| Uei | - | - | - | - | - | - | - | - | - | - | 1/1 | - | - | - | - | 1/1 |
| Karaurín | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0/0 |
| Total ETC | 1/2 | 1/3 | 1/4 | 5/5 | 1/1 | 2/10 | 2/3 | 7/16 | 2/7 | 1/1 | 3/7 | 2/2 | 2/8 | 1/3 | 1/2 | 32/74 |

Table 6. Plant species richness and degree of endemism of the ETC summits. Numbers of widely distributed Neotropical species and exotic species are provided. Tepuis are grouped according to species richness.

| | Sp. richness | Endemics | | | | Widespread | | Exotics |
|-----------|--------------|----------|-------------|-----|----------|----------------|------------|---------|
| | | Local | Summits ETC | ETC | Pantepui | Guayana Shield | Neotropics | |
| Roraima | 227 | 2 | 21 | 26 | 79 | 112 | 102 | 13 |
| Kukenán | 137 | 1 | 17 | 21 | 66 | 86 | 48 | - |
| Ilú | 128 | 4 | 18 | 23 | 60 | 81 | 46 | - |
| Yuruaní | 46 | - | 6 | 8 | 25 | 36 | 10 | - |
| Maringma | 40 | 1 | 2 | 4 | 15 | 30 | 8 | - |
| Tramen | 34 | - | 7 | 9 | 17 | 21 | 13 | - |
| Uei | 33 | 2 | 4 | 6 | 10 | 24 | 9 | - |
| Kaurín | 14 | - | 2 | 4 | 6 | 10 | 4 | - |
| Total ETC | 289 | 10 | 31 | 37 | 100 | 155 | 117 | 13 |

Table 7. Number of taxa by major plant group in the Venezuelan Guayana (VG), Pantepui, the ETC summits and the Roraima summit. A: angiosperms, P: pteridophytes.

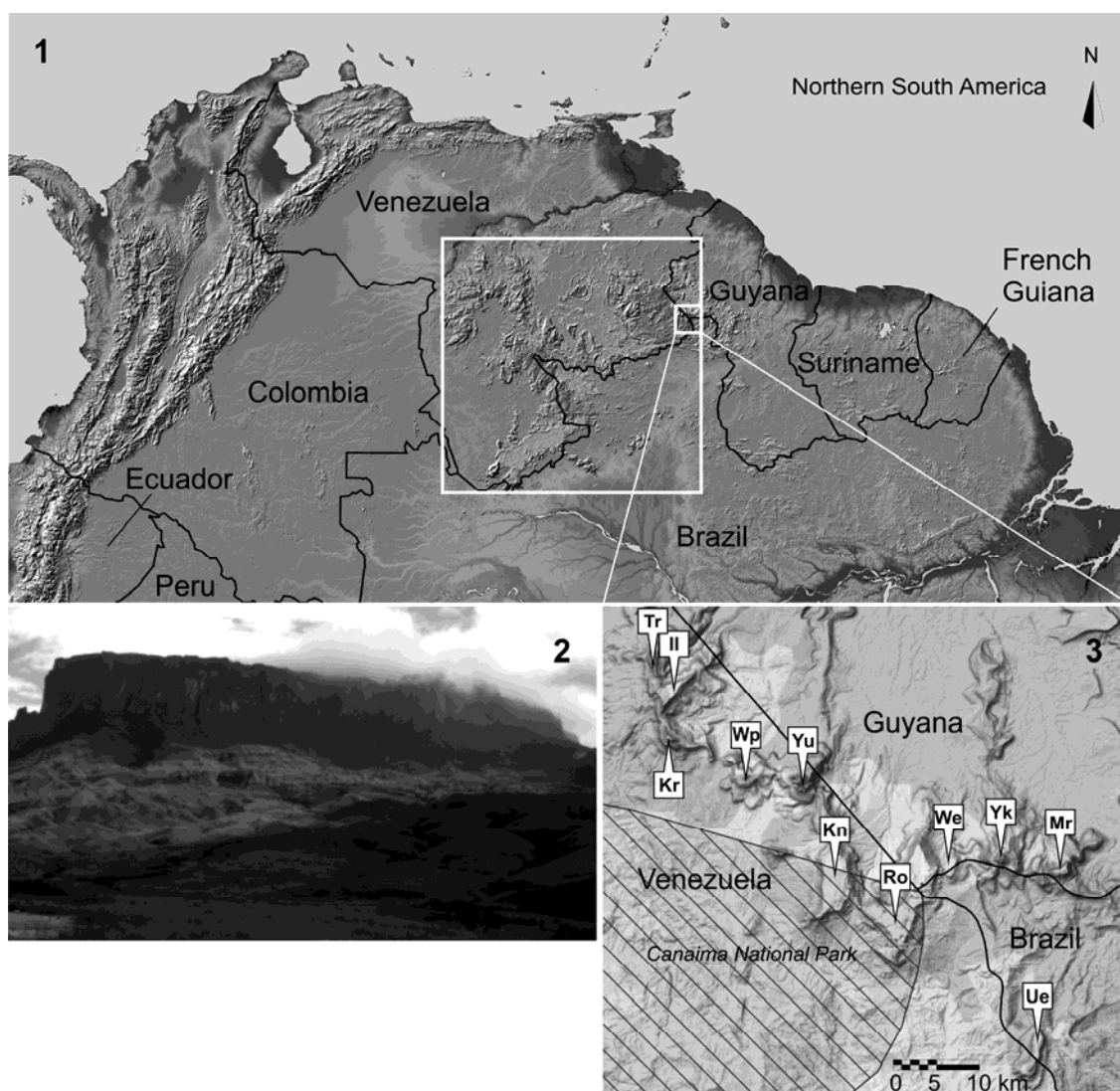
| | VG ^a | | Pantepui ^b | | ETC summits | | Roraima summit | |
|---------------|-----------------|-----------------|-----------------------|---------|-------------|---------|----------------|---------|
| | Genera | Species | Genera | Species | Genera | Species | Genera | Species |
| Gymnosperms | 3 | 21 ^c | 2 | 12 | - | - | - | - |
| Angiosperms | 1694 | 8740 | 1485 | 2097 | 119 | 215 | 99 | 157 |
| Pteridophytes | 92 | 671 | 155 | 324 | 32 | 74 | 31 | 70 |
| Ratio A/P | 18.41 | 13.03 | 9.58 | 6.47 | 3.72 | 2.91 | 3.19 | 2.24 |

^a From Berry et al. (1995).

^b From the Pantepui database (Nogué et al. 2009; Safont et al. 2012).

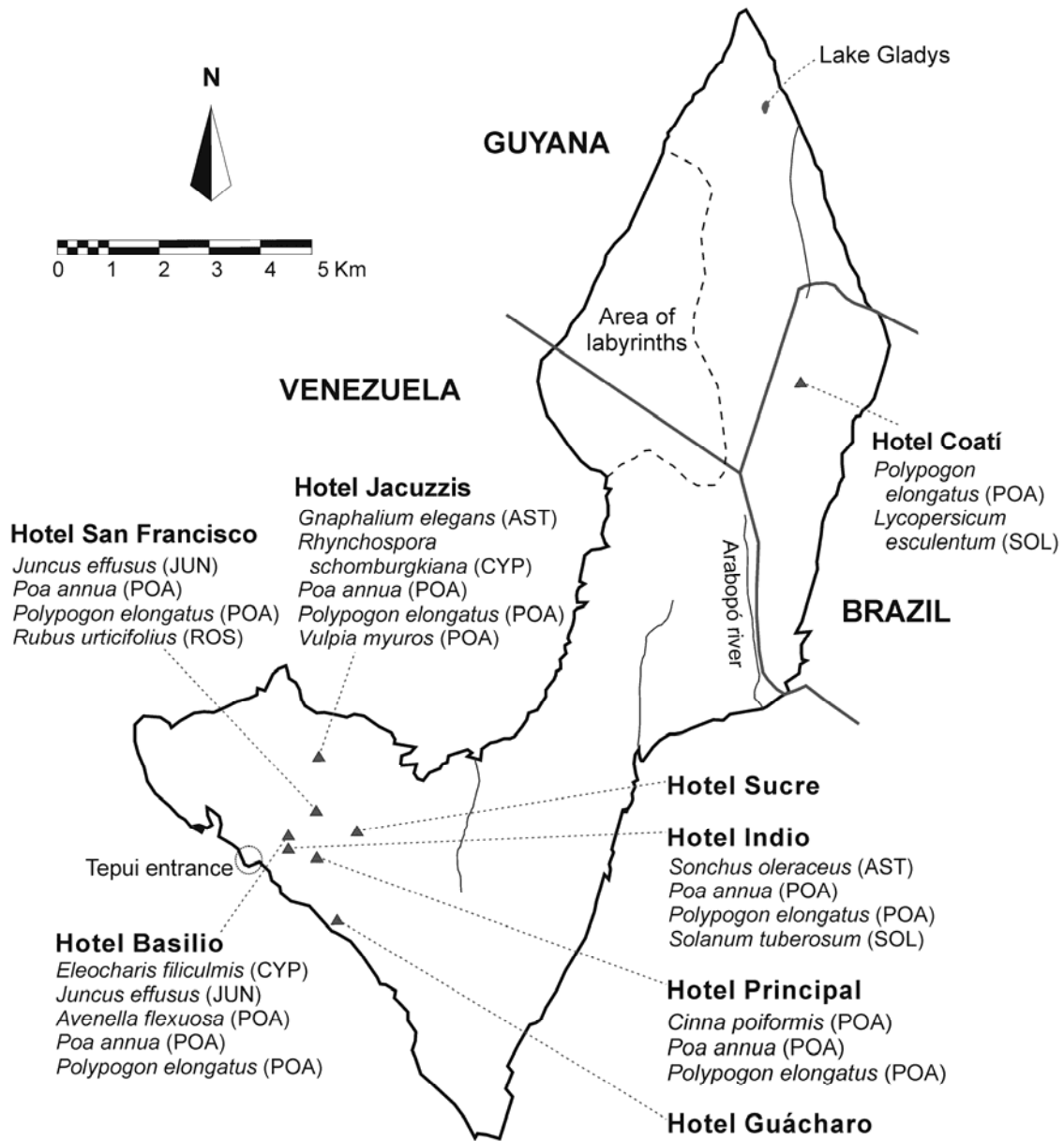
^c From Hokche et al. (2008).

Figures



Figs 1-3. Location of the study area. **1.** Map of northern South America showing the Pantepui province (larger white box) and location of the Eastern Tepui Chain (ETC) and Roraima-tepui (smaller white box). Radar image courtesy of NASA/JPL-Caltech. **2.** View of the Roraima-tepui from the Gran Sabana. Photograph: Yuribia Vivas. **3.** Extension of the ETC. Abbreviations of tepuis as in Table 1. Hash-mark area corresponds to Canaima National Park. Modified from Google Maps 2013.

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1371 **Fig. 4.** Location of exotic species found on the summit of Roraima-tepui, coinciding
 1372 with hotels and their surroundings. AST: Asteraceae, CYP: Cyperaceae, JUN:
 1373 Juncaceae, POA: Poaceae, ROS: Rosaceae, SOL: Solanaceae.

1374

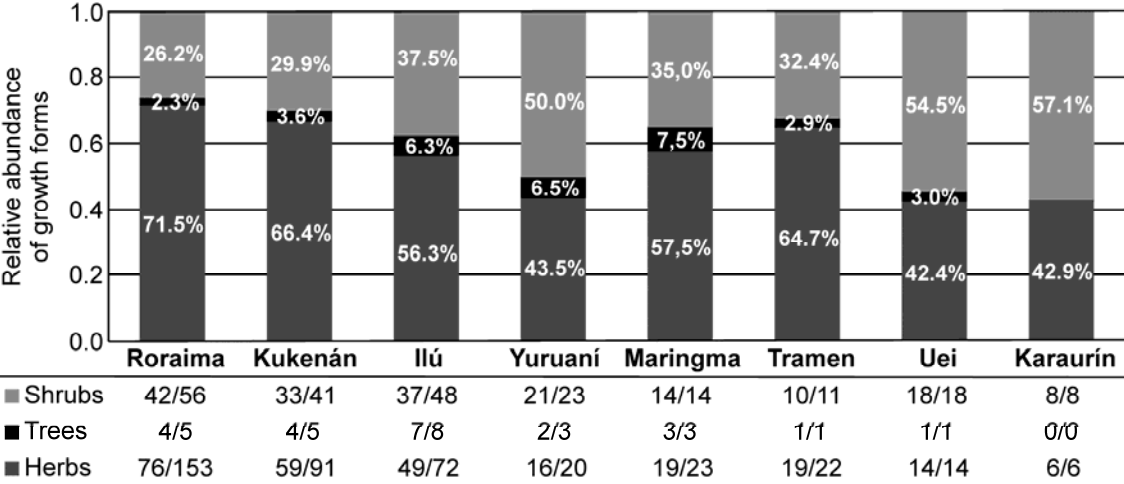


Fig. 5. Relative abundance of native species of herbaceous (dark gray), shrubby (light gray) and tree (black) growth forms in the tepui summits of the ETC. Diversity of genera and species are indicated before and after the slash, respectively.

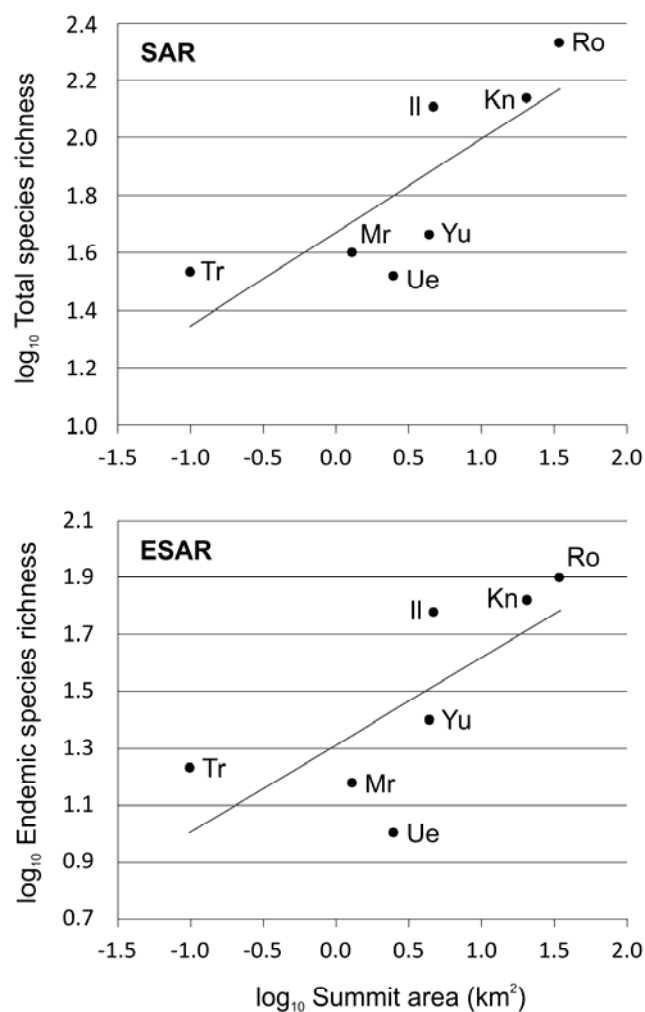


Fig. 6. Species-Area Relationship (SAR: $r^2 = 0.640$, $p = 0.031$) and Endemic Species-Area Relationship (ESAR: $r^2 = 0.516$, $p = 0.069$) for the ETC summits, with log-transformed data. Abbreviations of tepuis as in Table 1.

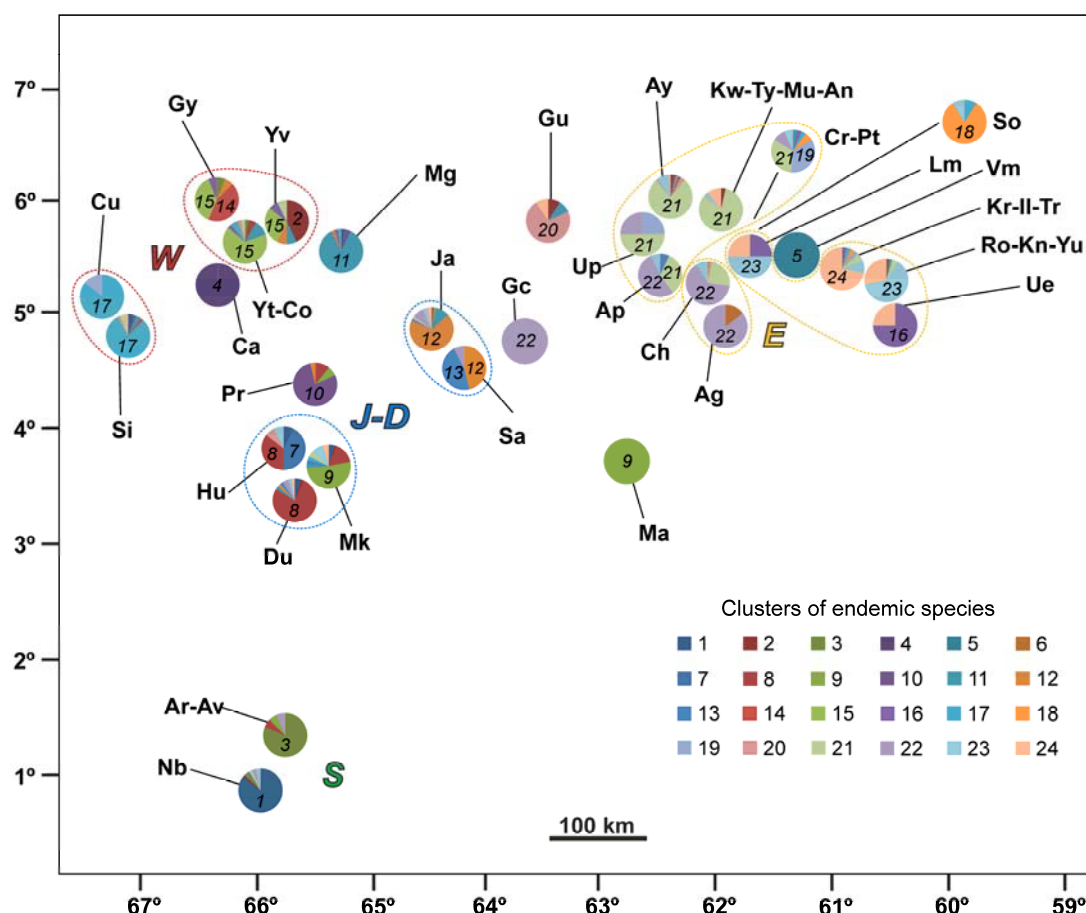


Fig. 7. Schematic map of Pantepui, showing the relative abundance of species clusters for each tepui/tepui massif (pie charts). Clusters were defined as groups of species with Raup-Crick similarity measure above 0.7. Dashed circles group the tepuis with highest floristic similarity within each district, based on Raup-Crick measure on the endemic species data matrix. **Eastern district (E):** Ag – Angasima, An – Aparamán, Ap – Aprada, Ay – Auyán, Ch – Chimantá, Cr – Carrao, Il – Ilú, Kn – Kukenán, Kr – Karaurín, Kw – Kamarkawarai, Lm – Lema, Mu – Murisipán, Pt – Ptari, Ro – Roraima, So – Sororopán, Tr – Tramen, Ty – Tereké-yurén, Ue – Uei, Ug – Upuigma, Up – Uaipán, Vm – Venamo, Yu – Yuruani; **Western district (W):** Ca – Camani, Co – Coro, Cu – Cuao, Gy – Guanay, Mg – Maigualida, Si – Sipapo, Yv – Yaví, Yt – Yutajé;

Jaua-Duida (J-D): Du – Duida, Hu – Huachamacari, Ja – Jaua, Mk – Marahuaka, Pr –
Parú, Sa – Sarisariñama; **Southern district (S):** Ar – Aracamuni, Av – Avispa, Nb –
Neblina. **Others:** Gc – Guanacoco, Gu – Guaiquinima, Ma – Marutaní.

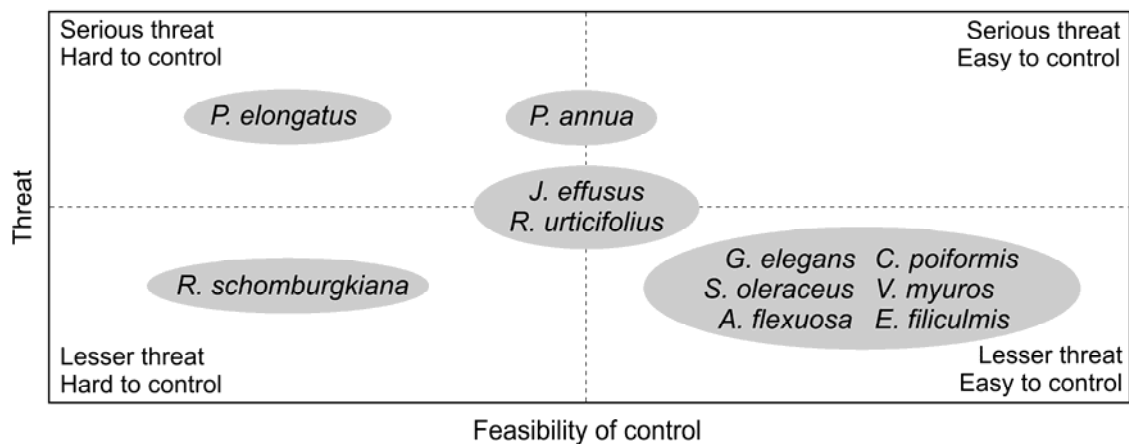


Fig. 8. Plot of level of potential impact vs. feasibility for control of exotic plant species on the Roraima summit (excluding casual exotics).

Online Resource 1

Supplemental material online to the paper “Establishing a baseline of plant diversity and endemism on a neotropical mountain summit for future comparative studies assessing upward migration: an approach from biogeography and nature conservation”, Systematics and Biodiversity, Safont, E., Rull, V., Vegas-Vilarrúbia, T., Holst, B.K., Huber, O., Nozawa, S., Vivas, Y. & Silva, A.

Appendix. List of the species of the Eastern Tepui Chain (ETC) summits, excluding those for which no floristic information is available (Wadakapiapué, Wei-Assipú and Yakontipú). Distribution within the ETC, exotic taxa and new reports are provided. Values in bold show the sum for each column. + sign is used to indicate the presence of the species in each summit, exotic species and new records, whereas ++ sign is used for species seen on the Roraima summit during our fieldwork (2011 and 2012). Taxon authors can be found through online sources such as TROPICOS (www.tropicos.org) or the International Plant Name Index (www.ipni.org).

[illegible]

| Major group | Family | Species | Infraspecifics on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Karaurín | Exotic species | New records for Roraima summit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|--------------|----------------------------------|---------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|--|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | Araliaceae | <i>Schefflera chimantensis</i> | ssp. <i>rugosifolia</i> | ++ | + | + | + | + | | | | | | | | | | |
| | | <i>Schefflera umbellata</i> | | ++ | + | + | + | | | | | | | | | | | |
| | Asteraceae | <i>Ageratina roraimensis</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Baccharis brachylaenoides</i> | | ++ | + | + | + | | + | + | | | | | | | | |
| | | <i>Baccharis densa</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Baccharis schomburgkii</i> | | ++ | | | | | | | | | | | | | | |
| | | <i>Calea lucida</i> | | | | + | | | | | + | | | | | | | |
| | | <i>Calea lucidivenia</i> | var. <i>cardonae</i> | | | + | | + | | | | | | | | | | |
| | | <i>Gnaphalium elegans</i> | | ++ | | | | | | | | + | + | + | + | + | | |
| | | <i>Gongylolepis benthamiana</i> | | | | + | | | | | | | | | | | | |
| | | <i>Guayania roupalifolia</i> | | ++ | + | + | + | | | + | | | | | | | | |
| | | <i>Koanophyllon fuscum</i> | | ++ | + | | | | | + | | | | | | | | |
| | | <i>Mikania boomii</i> | | | | | | + | | | | | | + | | | | |
| | | <i>Mikania lucida</i> | | ++ | | | | | | | | | + | | | | | |
| | | <i>Quelchia conferta</i> | | ++ | + | + | + | | | | | | | | | | | |
| | | <i>Sonchus oleraceus</i> | | ++ | | | | | | | | + | + | + | + | + | | |
| | | <i>Stenopadus connellii</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Stenopadus sericeus</i> | | ++ | | | | | | | | | + | + | | | | |
| | | <i>Stomatochaeta condensata</i> | | ++ | + | + | + | | | + | + | | | | | | | |
| | Bonnetiaceae | <i>Bonnetia roraimae</i> | | ++ | + | + | + | + | + | + | | | | | | | | |
| | | <i>Bonnetia tepuiensis</i> | | | | ? | + | | | ? | ? | | | | | | | |

| Major group | Family | Species | Infraspecifics on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Kaururín | Exotic species | New records for Roraima summit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|-------------|----------------------------------|---------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|--|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | Clusiaceae | <i>Clusia amabilis</i> | | | | | | + | | + | | | | | | | | |
| | | <i>Moronobea intermedia</i> | | | | + | | | | + | | | | | | | | |
| | Cunoniaceae | <i>Weinmannia brachystachya</i> | | | + | + | | | | | | | | | | | | |
| | | <i>Weinmannia fagaroides</i> | | ++ | | + | | | | | | | | | | | | |
| | | <i>Weinmannia glabra</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Weinmannia guyanensis</i> | var. <i>guyanensis</i> | ++ | | + | + | | + | | | | | | | | | |
| | | <i>Weinmannia ilutepuiensis</i> | | | | + | | | | | | | | | | | | |
| | | <i>Weinmannia laxiramea</i> | | ++ | + | | | | | | | | | | | | | |
| | Cyrillaceae | <i>Cyrilla racemiflora</i> | | ++ | + | + | + | + | + | + | + | | | | | | | |
| | Droseraceae | <i>Drosera hirticalyx</i> | | + | | | | | | | | | | | | | | |
| | | <i>Drosera kaieteurensis</i> | | | | | | + | | | | | | + | | | | |
| | | <i>Drosera roraimae</i> | | ++ | + | + | + | + | + | | + | | | | | | | |
| | | <i>Drosera solaris</i> | | | | | | + | | | | | | | | | | |
| | Ericaceae | <i>Bejaria imthurnii</i> | | ++ | + | + | + | | + | + | | | | | | | | |
| | | <i>Bejaria sprucei</i> | | | + | + | | | | | | | | | | | | |
| | | <i>Gaultheria erecta</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Gaultheria setulosa</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Ledothamnus guyanensis</i> | | | | | | | + | + | | | | | | | | |
| | | <i>Ledothamnus sessiliflorus</i> | | ++ | + | + | | + | + | | + | | | | | | | |
| | | <i>Pernettya marginata</i> | | ++ | + | + | + | | | | | | | | | | | |
| | | <i>Sphyraspermum cordifolium</i> | | ++ | + | + | | | | | | | + | | + | | | |

| Major group | Family | Species | Infraspecifics on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Karaurín | Exotic species | New records for Roraima summit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|------------------|----------------------------------|---------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|--|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | | <i>Tepuia tatei</i> | | | + | | + | | | | | | | | | | | |
| | | <i>Thibaudia nutans</i> | | ++ | + | + | + | | | | | | | | | | | |
| | | <i>Vaccinium corymbodendron</i> | | ++ | | | | | | | | | | | | | | |
| | | <i>Vaccinium roraimense</i> | | ++ | + | + | | | | | | | | | | | | |
| | Gentianaceae | <i>Celiantha imthurniana</i> | | ++ | + | + | | | + | | | | | | | | | |
| | | <i>Rogersonanthus quelchii</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Symbolanthus aureus</i> | | | | + | | | | | | | | | | | | |
| | | <i>Symbolanthus elisabethae</i> | | ++ | + | | | | | | | | | | | | | |
| | Hypericaceae | <i>Hypericum roraimense</i> | | ++ | + | | | | | | | | | | | | | |
| | Lentibulariaceae | <i>Genlisea pygmaea</i> | | | + | + | | | | | | | | | | | | |
| | | <i>Genlisea repens</i> | | ++ | + | | | | | | | | + | | | | | |
| | | <i>Genlisea roraimensis</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Utricularia amethystina</i> | | ++ | | | + | | + | | | | | | | | | |
| | | <i>Utricularia aureomaculata</i> | | | + | + | | | | | | | | | | | | |
| | | <i>Utricularia campbelliana</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Utricularia humboldtii</i> | | | | | | + | | | | | | + | | | | |
| | | <i>Utricularia pubescens</i> | | ++ | + | | | | | + | | | + | | | | | |
| | | <i>Utricularia quelchii</i> | | ++ | + | | + | | | | | | | | | | | |
| | | <i>Utricularia subulata</i> | | ++ | + | + | | | | | | | | | | | | |
| | Melastomataceae | <i>Marcetia taxifolia</i> | | ++ | | + | + | + | + | + | | | | | | | | |
| | | <i>Meriania crassiramis</i> | | | | | | + | | | | | | + | | + | | |

| Major group | Family | Species | Infraspecifcs on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Karaurín | Exotic species | New records for Roraima sumit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|-------------|-------------------------------|--------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|---|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | | <i>Miconia ciliata</i> | | | | | | | | + | | | | | | | | |
| | | <i>Miconia huberi</i> | | | | + | | | | | | | | | | | | |
| | | <i>Miconia rupestris</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Miconia</i> sp. | | ++ | | | | | | | | | | | | | | |
| | | <i>Miconia theaezans</i> | | | | + | | | | | | | | | | | | |
| | | <i>Miconia tinifolia</i> | | ++ | + | | | | + | | | | | | | | | |
| | | <i>Microlicia benthamiana</i> | | ++ | + | + | + | | + | + | | | | | | | | |
| | | <i>Monochaetum bonplandii</i> | | ++ | | + | | | | + | | | | | | | | |
| | | <i>Tibouchina</i> sp. | | ++ | | | | | | | | | + | + | + | + | | |
| | Myrsinaceae | <i>Cybianthus crotonoides</i> | | | | | | + | | | | | | + | | | | |
| | | <i>Cybianthus lineatus</i> | | | + | | | | | | | | | | | | | |
| | | <i>Cybianthus ptiariensis</i> | | | | + | + | | | | | | | | | | | |
| | | <i>Cybianthus quelchii</i> | | ++ | + | | + | | | + | | | | | | | | |
| | | <i>Cybianthus roraimae</i> | | | | + | | | | | | | | | | | | |
| | | <i>Myrsine guianensis</i> | | | | + | | | | | | | | | | | | |
| | | <i>Myrsine minima</i> | | ++ | + | + | | | | | | | | | | | | |
| | Myrtaceae | <i>Myrcia tepuiensis</i> | | | | + | | | | | | | | | | | | |
| | | <i>Ugni myricoides</i> | | ++ | + | + | + | + | + | | + | | | | | | | |
| | Ochnaceae | <i>Adenanthe bicarpellata</i> | | | | | | + | | | | | | + | | + | | |
| | | <i>Poecilandra retusa</i> | var. <i>sclerophylla</i> | | | + | + | + | | | + | | | | | | | |
| | | <i>Sauvagesia imthurniana</i> | | ++ | + | + | + | | + | | + | | | | | | | |

| Major group | Family | Species | Infraspecifics on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Karaurín | Exotic species | New records for Roraima sumit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|----------------|----------------------------------|---------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|---|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | Passifloraceae | <i>Passiflora sclerophylla</i> | | | | | | | | + | | | | | | | | |
| | Phyllanthaceae | <i>Phyllanthus pycnophyllus</i> | | | | | | | | + | | | | | | | | |
| | Piperaceae | <i>Peperomia acuminata</i> | | ++ | | | | | | | | | | | | | | |
| | | <i>Peperomia delascioi</i> | | ++ | | + | | | | | | | | | | | | |
| | | <i>Peperomia galioides</i> | | ++ | | + | | | | | | | | | | | | |
| | | <i>Peperomia rotundata</i> | var. <i>rotundata</i> | ++ | | + | | | | | | | + | | | | | |
| | | <i>Peperomia tenella</i> | var. <i>tenella</i> | ++ | + | + | | | | | | | | | | | | |
| | Polygalaceae | <i>Monnina cacumina</i> | | ++ | | | | | | + | | | | | | | | |
| | Polygonaceae | <i>Coccoloba schomburgkii</i> | | | | + | | | | + | | | | | | | | |
| | Rhamnaceae | <i>Rhamnus ulei</i> | | ++ | | | | | | | | | + | + | + | + | + | + |
| | Rosaceae | <i>Hesperomeles obtusifolia</i> | var. <i>obtusifolia</i> | ++ | | + | | | | | | | + | | + | | + | |
| | | <i>Rubus urticifolius</i> | | ++ | | | | | | | | + | + | + | + | + | + | |
| | Rubiaceae | <i>Maguireothamnus speciosus</i> | ssp. <i>speciosus</i> | ++ | + | | + | + | | | | | | | | | | |
| | | <i>Notopleura crassa</i> | | ++ | + | + | + | | | | | | | | | | | |
| | | <i>Notopleura tapajozensis</i> | | | | | | + | | | | | | + | | | | |
| | | <i>Pagamea magniflora</i> | | | | + | | | | | | | | | | | | |
| | | <i>Palicourea obtusata</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Psychotria aubletiana</i> | | ++ | | + | | | | | | | + | | | | | |
| | | <i>Psychotria concinna</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Psychotria everardii</i> | | | | | + | + | | | | | | | | | | |
| | | <i>Psychotria glandulicalyx</i> | | | | | | | | | + | | | | | | | |

| Major group | Family | Species | Infraspecifics on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Karaurín | Exotic species | New records for Roraima sumit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|---------------|------------------------------------|---------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|---|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | | <i>Syngonanthus duidae</i> | var. <i>humilis</i> | + | + | | | | | + | | | | | | | | |
| | | <i>Syngonanthus pakaraimensis</i> | var. <i>pakaraimensis</i> | | | + | | | | | | | | | | | | |
| | Juncaceae | <i>Juncus effusus</i> | | ++ | | | | | | | | + | + | + | + | + | + | + |
| | Nartheciaceae | <i>Nietneria corymbosa</i> | | ++ | + | | + | | | | | | | | | | | |
| | | <i>Nietneria paniculata</i> | | + | | | | | | | | | | | | | | |
| | Orchidaceae | <i>Brachionidium longicaudatum</i> | | ++ | + | | | | | | | | + | | | | | |
| | | <i>Bulbophyllum roraimense</i> | | + | | | | | | | | | | | | | | |
| | | <i>Cleistes huberi</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Cleistes parviflora</i> | | ? | | | | | | | | | | | | | | |
| | | <i>Crocodeilanthus moritzii</i> | | ++ | + | | | | | | | | + | | | | | |
| | | <i>Elleanthus confusus</i> | | ++ | + | | | | | | | | + | + | + | + | | |
| | | <i>Epidendrum alsum</i> | | ++ | | | | | | | | | | | | | | |
| | | <i>Epidendrum attenuatum</i> | | ++ | | | | | | | | | + | + | | | | |
| | | <i>Epidendrum imthurnii</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Epidendrum montigenum</i> | | ++ | + | + | | | + | | | | | | | | | |
| | | <i>Epidendrum reclinatum</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Epidendrum</i> sp. | | ++ | | | | | | | | | + | + | | | | |
| | | <i>Epidendrum violascens</i> | | ++ | + | + | | | + | | | | | | | | | |
| | | <i>Eriopsis biloba</i> | | ++ | + | + | + | | | | | | + | | + | | | |
| | | <i>Gomphichis adnata</i> | | ++ | | | | | | | | | + | + | + | + | | |
| | | <i>Habenaria parviflora</i> | | | | | | | | + | | | | | | | | |

| Major group | Family | Species | Infraspecifics on Roraima | Roraima | Kukenán | Ilú | Yuruaní | Maringma | Tramen | Uei | Karaurín | Exotic species | New records for Roraima summit since FVG | New species for ETC summits | New genus for Roraima summit | New genus for ETC summits | New family for Roraima summit | New family for ETC summits |
|-------------|---------|----------------------------------|---------------------------|---------|---------|-----|---------|----------|--------|-----|----------|----------------|--|-----------------------------|------------------------------|---------------------------|-------------------------------|----------------------------|
| | | <i>Habenaria roraimensis</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Helonoma bifida</i> | | + | + | | + | | | | | | | | | | | |
| | | <i>Lepanthes unitrinervis</i> | | ++ | | + | | | | | | | | | | | | |
| | | <i>Maxillaria mapiriensis</i> | | | + | | | | | | | | | | | | | |
| | | <i>Maxillaria meridensis</i> | | | + | | | | | | | | | | | | | |
| | | <i>Maxillaria quelchii</i> | | ++ | | + | | | | | | | | | | | | |
| | | <i>Octomeria connellii</i> | | ++ | + | + | | | + | | | | | | | | | |
| | | <i>Octomeria flaviflora</i> | | + | + | | | | | | | | | | | | | |
| | | <i>Octomeria monticola</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Octomeria parvifolia</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Octomeria</i> sp. | | ++ | | | | | | | | | | | | | | |
| | | <i>Prescottia carnosa</i> | | ++ | + | + | | | | | | | | | | | | |
| | | <i>Stelis</i> sp. | | | + | | | | | | | | | | | | | |
| | | <i>Trichosalpinx roraimensis</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Trichosalpinx</i> sp. | | ++ | | | | | | | | | + | + | | | | |
| | | <i>Zygosepalum angustilabium</i> | | | + | | | | | | | | | | | | | |
| | Poaceae | <i>Aulonemia deflexa</i> | | ++ | | + | | | | | | | | | | | | |
| | | <i>Avenella flexuosa</i> | | ++ | | | | | | | | + | + | + | + | + | | |
| | | <i>Axonopus caulescens</i> | | | | | | | | + | | | | | | | | |
| | | <i>Chusquea linearis</i> | | ++ | + | | | | | | | | | | | | | |
| | | <i>Cinna poiformis</i> | | ++ | | | | | | | | + | + | + | + | + | | |

